The concealed copulatory structures of the *Pyrgomorphidae* (Orth. Acridoidea)

PART I. GENERAL INTRODUCTION

BY

D. KEITH MCE. KEVAN, SYED S. AKBAR [1] and YU-CHENG CHANG [2].

Macdonald College, P. Quebec, Canada.

ABSTRACT.

The mainly tropical and subtropical acridoid family *Pyrgomorphidae* includes over 140 genera grouped in 30 tribes. The present work serves as a general introduction to a comparative morphological study of the phallic structures, female subgenital armature and receptacula seminis of every tribe and almost every known genus and subgenus. A general account and literature review in respect of the acridoid phallic complex are given and the special features of the *Pyrgomorphidae* are discussed. An attempt is made to homologize phallic terminology throughout the *Acridoidea*. A synopsis of the phallic characters of the *Pyrgomorphidae* in general is given. A general account and literature review are also given in respect of the female subgenital armature and receptaculum seminis of the *Acridoidea*, with special reference to the *Pyrgomorphidae*. In discussing the receptaculum seminis, different orthopteroid orders are considered with particular reference to the bifid or paired nature of the organ and the various modifications as they occur throughout the group. The paired condition is believed to be primitive in *Dictyoptera, Isoptera* and *Orthoptera, s. str.* In the last order, parallel variations exist within the suborders *Ensifera* and *Caelifera*, particularly *Pyrgomorphidae*. The homologies in the receptaculum seminis throughout the different families of *Acridoidea* are discussed and a hypothetical generalized form of the organ is illustrated. Terminology is reviewed and revised for both subgenital armature and receptaculum seminis. Synonymic glossaries of the terms adopted in the present studies for both male and female genitalic structures in the *Pyrgomorphidae* are given. For the most part the terms

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[1] Present address: Department of Zoology, University of Sind, Jamshoro, West Pakistan.

[2] Present address: Tobacco Research Institute, Tsao-Hu, Taichung, Taiwan.

used are generally applicable throughout the *Acridoidea,* although there are a few structures that are peculiar to *Pyrgomorphidae.* Some structures found in other groups are absent in *Pyrgomorphidae.*

EXPLANATION.

The general account of the male structures is based largely upon part of the doctoral thesis of Akbar (1963), from which the majority of the figures of phallic structures to be used in subsequent parts of this study (except for those of genera subsequently added to the *Pyrgomorphidae* and a few others that have become available for study more recently) have been taken. Support was received from the Colombo Plan through the External Aid Office, Ottawa, and from the National Research Council of Canada.

The account of the females incorporates material from the master's thesis of Chang (1966), from which most of the figures of the female structures (except for those genera that have become available subsequently) have been adapted. Support was received from the National Research Council of Canada.

1. INTRODUCTION.

The Superfamily *Acridoidea,* to which the *Pyrgomorphidae* belong, is here understood in the same sense as by Uvarov (1966). It excludes the formerly included families *Tetrigidae, Pneumoridae, Tanaoceridae, Eumastacidae* and *Proscopiidae.* Uvarov regards each of these as constituting a separate superfamily. The last two, however, were grouped into a single superfamily *(Eusmastacoidea)* by Kevan (1966 h) on morphological grounds (see also Blackith and Blackith, 1966 b); they are also similar in chromosome number (2n ♂ = 17) and form (Miss C. E. Albizu, *in litt.,* 1966) [3].

Within the *Acridoidea,* the family *Pyrgomorphidae* constitutes a group of 'bush-hoppers', mainly tropical and subtropical in distribution. Some 143 genera and seven subgenera disposed in 30 tribes are now recognized. The number of species is uncertain, as the taxonomy of several of the larger genera remains in a chaotic state, but it considerably exceeds 400. A general account of the family, its taxonomic history, geographical distribution and suprageneric taxonomy, has been

[3] Dirsh (1966 b) also groups these two families together, but further places the *Tanaoceridae* in the *Pneumoroidea* and removes the *Xyronotidae* from the *Acridoidea* to the same superfamily. *Trigonopterygidae* are also removed from the *Acridoidea* and given superfamily rank.

given by Kevan and Akbar (1964). Only slight modifications of the scheme of classification presented by these authors have subsequently been published, mostly resulting from the erection of new genera or from the transference of others to the *Pyrgomorphidae* from the *Acrididae* (Kevan, 1964 b, 1966 b, d-h and 1968 b; Descamps and Wintrebert, 1966 a, b). No major change is proposed in the present work, although, in subsequent parts, there will be some minor ones and considerable rearrangement of the sequence of tribes.

The grouping by Kevan and Akbar *(op. cit.)* of the various genera into tribes and subtribes was based upon a consideration of both external anatomy and phallic morphology, although few details of the latter were given. Papers illustrating the phallic complexes of a number of genera of *Pyrgomorphidae* in greater detail than elsewhere, most of them using much of the terminology adopted in the present work, have appeared in advance of this study (Kevan and Akbar, 1963, 1964; Akbar and Kevan, 1964; Kevan, Akbar and Singh, 1964; Kevan, Singh and Akbar, 1964 a, b; Kevan, 1964 a, b, 1965, 1966 a, b, d-g, i, 1967 a; Singh and Kevan, 1965; Akbar, 1966 a, b; Descamps and Wintrebert, 1966 b, 1968 b), and others published too recently for inclusion here, but in most of these the structures have been used only as a basis for comparison between genera or species; no detailed discussion of the structures themselves has been presented, except to a small degree by Akbar (1966 b). The female copulatory structures of *Pyrgomorphidae* have also proved to be of taxonomic value and have been illustrated for several genera (Randell, 1963; Kevan, 1963; 1966 a, b, e-g, i, 1967 a, 1968 b; Akbar, 1966 a; Descamps and Wintrebert, 1966 b) and others more recently, but again, except for the preliminary observations of Randell and Akbar *(opera cit.)* no recent general discussion has been published.

The present work will attempt to review comparatively, in-so-far as possible, the chitinous, particularly the sclerotized, parts of the phallic complex, the female subgenital armature and the receptaculum seminis (spermatheca of many authors) of every known genus of *Pyrgomorphidae,* in order to establish the relationships existing between them. It was also hoped to deduce something of their phylogeny within the family. The latter, however, has proved very difficult because of the way in which almost any given structure may differ in its degree of modification as between groups of genera without corresponding differences being apparent for other structures, either in the same or the

opposite sex. The grouping of genera into tribes, and even subtribes, has not, for the most part, proved too difficult, particularly if both external and 'concealed' characters are taken together, but the relationships between many of the tribes have been far from conclusively established.

By and large, groupings recognized on the basis of phallic characters have been well supported, or at least have not been disturbed, by a study of the female organs, although a few anomalies remain. As the female structures are simpler than those of the males, and show correspondingly less variation, there would, perhaps, if these alone were considered, be justification for dividing the *Pyrgomorphidae* into fewer tribes than are currently recognized. Contrarily, however, within certain tribes, notably *Desmopterini* and *Nereniini* there exist group differences among genera, which are clearer between females than between males to the extent that, were the female structures the only characters used, some of the genera in question would be placed in quite separate tribes. Similarity between females does not always reflect similarity between males, and *vice versa,* although it usually does so. It has generally been possible to place in their appropriate tribes those genera for which only the female is known, and, in some instances, it has also been possible, on the basis of female characters, to place with less uncertainty, genera whose phallic structures are anomalous.

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2. Materials and methods.

With very few exceptions, the concealed genitalia of both sexes of every known genus and subgenus of *Pyrgomorphidae* have been examined. Exceptions are as follows:

Males: *Kuantania* Miller, *Oxytarbaleus* Ramme, *Spinacris* Willemse, *Paradoriaella* Willemse, *Paraphymateus* Dirsh, *Deraspiella* Bolívar, *Petaside* White, *Carinisphena* Kevan, *Geloiodes* Chopard and *Caconda* Bolívar; no male is known for any of these genera:

Females: *Fijipyrgus* Kevan, *Sagittacris* Dirsh, *Parorthacris* Dirsh, *Pterorthacris* Uvarov, *Katangacris* Kevan and *Marsabitacris* Kevan; no female is known for any of these genera.

Both sexes: *Buyssoniella* Bolívar and *Moxicus* Kevan; in the first of these, the unique female holotype has been lost; in *Moxicus,* the only adult female (holotype) has not been made available for dissection, and, in the only known male (allotype — ? immature), the phallic structures do not seem to have developed. *Moxicus,* in any event, is probably best considered as being synonymous with *Caconda* and has been so regarded (without explanation) by Dirsh (1965 b, 1966 b). *Miopyrgomorpha* Kevan, being fossil, could not be examined either.

Most of the material examined (virtually all of which was dry-pinned) is in the collection of the most senior author and currently in the Lyman Entomological Museum. Some specimens (many of them

paratypes or even holotypes), however, had to be borrowed from the other institutions indicated in the Acknowledgements.

Phallic structures were extracted for examination in the same general way as described by Hubbell (1932) and Roberts (1941), although the method of softening the abdominal terminalia was not usually by immersing these in hot water, but by relaxing the whole insect over water (to which a few crystals of phenol had been added) in a small desiccator. Gurney and Brooks (1959), Barnum (1959) and Hubbell (1960) used similar methods. Depending upon the size of the insect, and upon its age and general state of preservation, the period of relaxation was usually about 24 hours, but varied up to several days. This method was always preferred for fully alate and most brachypterous species, as the quicker hot water treatment (which was, however, often used for micropterous and apterous species) is very liable to distort or discolour the wings.

Once removed from the insect, the phallic structures were placed in hot 10 per cent. potassium hydroxide (up to about 70° C.) for a variable period, depending upon such factors as already mentioned (usually about 10 minutes), to remove unsclerotized and non-chitinous tissues. They were then thoroughly washed in tap water and examined in glycerol on a cavity slide (without a coverglass), using a binocular, or occasionally a compound, microscope. Glycerol was preferred to 70 per cent. ethyl alcohol as a mountant for two principal reasons. Firstly, this medium cleared the structures to a suitable degree, and, secondly, it did not evaporate significantly, either on a slide under a strong microscope lamp, or in the microvials to which the specimens were later transferred for storage. The microvials were pinned through their stoppers beneath the insects from which the phallic structures had originally been extracted.

Drawings were initially made by means of a microprojector (Ken-A-Vision Manufacturing Co., Inc., Raytown, Missouri), details being filled in by conventional microscope examination. Difficulty in maintaining proper orientation of the specimens was overcome by supporting them in the required position with small pieces of absorbent cotton fibre or tiny slivers of cellophane (cover-glass fragments were less satisfactory). The entire phallic complex was drawn from dorsal, ventral and lateral views. The ectophallic membrane, along with the attached epiphallus was then removed by means of fine needles and the latter drawn separately. The endophallus was withdrawn through the

anterior part of the cingulum and drawn from dorsal, ventral and lateral aspects. As far as was practical, the phallic structures of all genera were drawn to one scale, but several specimens of very small or very large size were drawn to different uniform scales, as will be indicated in the illustrations. The ectophallic membrane in all figures is outlined by a dotted line; other membranous structures (notably the central membrane of the ectophallus) are stippled; solid black is used occasionally to indicate small regions of greater (not necessarily heavy) sclerotization; parts covered by others, but which it is desired to show, are outlined by broken lines. In all figures the anterior portions of the structures are directed towards the top of the page, or to the right in lateral views.

The preparation of the female structures and their subsequent treatment were basically similar to those described for the phallic complex. The removal of the subgenital plate was done in the manner indicated by Randell (1963), which results in very little obvious damage to a specimen. Considerable care was taken to ensure that the posterior end of the spermathecal duct was removed together with the rest of the receptaculum seminis. The operation was performed by cutting the roof of the genital chamber where the spermathecal duct joins the chamber. This usually involved the cutting and separation of the inner bases of the ventral ovipositor valves. As the operation was very delicate it proved impossible in a few instances in the earlier stages of the work to remove the posterior part of the duct without damage. The coils of the spermathecal duct were loosened or unravelled before drawing.

Differences in treatment between male and female structures were as follows: the receptaculum seminis (but not the subgenital plate) was usually cleared by means of 5 (not 10) per cent. potassium hydroxide, and a cover-glass over the cavity of the slide was normally used when examining the subgenital plate. This was to prevent the latter from curling upwards and inwards at the edges. The drawings of this structure will thus show it, in many instances, in a slightly (but not unduly) more flattened state than in its natural position. Two uniform scales only were used for the female structures, depending upon the relative size of the subgenital plate.

3. The acridoid phallic complex, with special reference to the Pyrgomorphidae.

a) *General Remarks.*

The phallic structures of *Acridoidea* have been the subject of investigation by numerous authors over a long period. Some of the investigations have been restricted to a few species only; others have more comprehensive. Some have been comparative anatomical studies; others have been basically or entirely systematic in approach. It is not appropriate here to attempt to cover the whole literature on the field, particularly as most of the older, largely unsound, accounts have been reviewed in the major works of Peytoureau (1895) and Chopard (1920). Roberts (1941) and Dirsh (1956) give comparative reviews of publications since Chopard *(l. c.)*. The following, in chronological order, are among those that have been consulted during the present study: Brunner von Wattenwyl (1876), Packard (1878), Berlese (1882), Peytoureau (1895), Berlese (1906), Crampton (1918), Chopard (1920), Walker (1922), MacGillivray (1923), Baranov (1925), Znoĭko (1928), Boldȳrev (1929), Hubbell (1932), Else (1934), Silvestri (1934), Guarino (1935), Snodgrass (1935 a, b), Jannone (1936, 1937), Snodgrass (1937), Jannone (1939), Gurney (1940), Qadri (1940), Roberts (1941), Karandikar (1942), Uvarov (1943), Grassé and Hollande (1945, 1946), Chopard (1949), Ohmachi (1950), Albrecht (1953), Beier (1955), Albrecht (1956), Ander (1956), Dirsh (1956), Lux (1957), Snodgrass (1957), Barnum (1959), Latif *et al.* (1959), Rehn and Grant (1959 a-c, 1960 a-c), Hubbell (1960), Dirsh (1961), Eades (1961 a, b), Gurney and Eades (1961), Lal and Parshad (1961 a, b), Lux (1961), Rehn and Eades (1961 a-d), Uvarov and Dirsh (1961), Dirsh (1962, 1963 a-c), Eades (1962, 1963), Márquez Mayaudón (1967), Jago (1963), Dirsh (1963 c, 1964 a, 1965 b, c), Gregory (1965), Thomas (1965), Descamps (1966), Descamps and Wintrebert (1966 b), Dirsh (1966 a, b), Kevan (1966 c), Uvarov (1966), Vickery (1967 a, b), Bigelow (1968), Descamps (1968) and several others received subsequent to going to press, together with the numerous papers on *Pyrgomorphidae* referred to in the third paragraph of the introduction (p. 167), particularly those of Kevan and Akbar (1963, 1964), Akbar (1966 b) and Kevan (1966 g). Apart from these last, the only works among those cited above that

deal directly with *Pyrgomorphidae* are those of Chopard (1920), Roberts (1941), Dirsh (1956, 1961, 1963 b, 1964 a, 1965 b, 1966 b), Latif *et al.* (1959), Márquez Mayaudón (1967), Descamps and Wintrebert (1966 b) and, to a small extent, Eades (1961 b).

As has been noted on more than one occasion by Snodgrass, the orthopteroid orders are 'genitalic individualists', and it has proven difficult, if not impossible, to homologize all their phallic structures with those of other insects. This is because, in most orders of insects, the phallic lobes divide vertically during development, whereas in orthopteroid insects they divide transversely. Even within these orders there has been a great diversity and multiplication of terms, with a corresponding imprecision and lack of uniformity, as reference to Tuxen (1956) and Randell (1964) will show. It is beyond the scope of the present work to attempt to establish homologies for the phallic structures of all *Orthoptera,* let alone of other orders, but in-so-far as it is appropriate to the *Pyrgomorphidae* the terminology here used is applicable on a homologous basis to all *Acridoidea.* Terms of convenience used only for structures peculiar to *Pyrgomorphidae* will be indicated as such.

Following Chopard's (1920) classic comparative work on the genitalia of orthopteroid insects generally, the morphological study of the phallic complex of *Dissosteira carolina* (Linnaeus) *(Acrididae)* by Walker (1922), further elaborated by Snodgrass (1935 a, 1937), helped much in formulating a generalized phallic terminology for the *Acridoidea.* Roberts (1941), Grassé and Hollande (1946), Dirsh (1956) and Eades (1961 a, b, 1962, 1963) [4] have subsequently each made efforts to clarify the homologies involved and to rationalize terminology. Most of the terms used herein for the *Pyrgomorphidae* have been adopted from Roberts, Dirsh and Eades. The choice of term has generally been on the basis of precision of definition or appropriateness; priority of usage has been given secondary consideration. A few structures not previously described (or at least not named) in this or other families have new terms proposed for them, as their homologies, if any, are un-

[4] Dirsh (1965 b, 1966 b) merely repeats his previous terminology without reference to the works of Eades *(ll. cc.).* Many other authors, including Uvarov and Dirsh (1961), Gregory (1965), Uvarov (1966) and Bigelow (1968), also adhere generally to Dirsh's terminology, Uvarov stating only that Eades (1961 b) "introduced further changes which are, however, debatable"; no grounds for this bald stament are given, nor has any hint of a debate so far been published.

known. Several of these terms have already been introduced into the literature in advance of the present study, e. g., by Kevan and Akbar (1963, 1964) and Akbar (1966 b). Terms relating to the acridoid phallic complex, but which are not applicable to *Pyrgomorphidae,* are not considered here. Definitions and synonyms of the terms used will be found on pp. 221-240.

b) *The Phallic Complex as a Whole.*

The phallic complex of *Acridoidea* in general, and of *Pyrgomorphidae* in particular, is basically a bulb-like organ, heavily sclerotized to a greater or lesser extent, and located within the genital chamber (Fig. 1, *D,* GC). Dorsally, it is covered partly by the paraprocts (PR) and epiproct (EP) and partly by the pallium (PL); lateroventrally it is surrounded by the ninth abdominal sternum (IX S), the terminal part of which forms the subgenital plate (SP). There are three distinct parts to the phallic complex: epiphallus, ectophallus and endophallus. Snodgrass (1937) and Qadri (1940) showed that the genitalia of orthopteroid insects arise from a single pair of primary rudiments, the phallic lobes, which develop around the orifice of the ejaculatory duct. These split transversely (horizontally) into two dorsal and two ventral phallomeres. The latter follow special lines of development in different groups of *Orthoptera* (Snodgrass, 1957; Randell, 1964). As indicated by Dirsh (1956) the entire structure is ectodermal in origin and develops from the ejaculatory duct which first forms a large endophallic cavity. The distal parts of the endophallic membrane continue to grow upwards and give rise to the ectophallic membrane. In highly developed forms the endophallic membrane proper differentiates into spermatophore sac, ejaculatory sac and endophallic sclerites, whereas the ectophallic membrane forms the cingulum and epiphallus. Randell (1964) presents evidence that the epiphallus (or most of it) represents the sternum (or a portion thereof) of the tenth abdominal segment, although Karandikar (1942) suggests the eleventh. The epiphallus, ectophallus and endophallus show various degrees of development and differentiation within the *Acridoidea.*

Although *Pyrgomorphidae* were included in the general studies of Chopard (1920), Roberts (1941), and Dirsh (1956), the first detailed description of the phallic structures of a member of the family *per se,*

was that of Latif *et al.* (1959) for *Poekilocerus pictus* (Fabricius), of which a revised account is given by Akbar (1966 b). The principal characteristics in the *Pyrgomorphidae* are summarized by Kevan and Akbar (1964).

c) *The Epiphallus.*

The epiphallus of all *Acridoidea, sensu stricto,* is a strongly sclerotized structure located on the dorsal surface of the ectophallus, except in *Trigonopterygidae* where it has moved to a ventral position (see Dirsh, 1952; 1956; 1961; Kevan, 1966 c). Roberts (1941) described three general forms of epiphallus, one distinctive for *Pyrgomorphinae* (now *Pyrgomorphidae),* one for *Pamphaginae* and its allied "subfamilies" (now *Pamphagidae)* — these two belonging to his group *Chasmosacci* — and one for the remaining "subfamilies" — *Cryptosacci.* Dirsh (1956), on the other hand, considered that there are only two principal forms, the one plate-like *(Xyronotidae* and *Trigonopterygidae,* occurring also in *Tanaoceroidea* and *Pneumoroidea,* i. e. not in *Acridoidea, sensu* Dirsh (1966 b)) or shield-like *(Charilaidae* [= *Pamphagodidae*] [5] and *Pamphagidae),* and the other bridge-like (as in the remaining families). The epiphalli of *Eumastacoidea,* show a much greater diversity of form (Dirsh, 1956, 1961, 1964 b; Rehn and Grant, 1958; Descamps, 1964).

The bridge-like epiphallus (Fig. 1, *A),* in its essential features, is composed of a pair of lateral plates (LP) connected with one another by a median plate, the bridge (B) (which is membranous in *Ommexechidae)* [6]. The lateral plates may be narrow or broad and bear pairs of projections (AP and PP) on their anterolateral and posterolateral margins. The bridge, likewise, may be narrow or broad and in some *Acrididae* may be interrupted along the median line (some *Catantopinae, Euryphyminae* and *Hemiacridinae).* It may also bear a pair of projections, the ancorae (AN), on its anterior border, and another pair, the lophi (L), on its posterior margin (the latter are invariably absent in shield- or plate-like epiphalli). A pair of small, oval or irregularly shaped sclerites (OS) usually lie on the lateral margins of the epiphallus, but most often remain separate from them, although they are very

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[5] Reunited with the *Pamphagidae* by Eades (1963); see also Descamps (1966).

[6] Eades (1961 a) has denoted this family to be a subfamily of *Acrididae.*

close to the lateral plates in *Ommexechidae* and *Lentulidae,* and attached to them in *Lathiceridae.* In *Pyrgomorphidae* (Fig. 1, *B*), what appear to be homologous structures are also attached to the lateral plates, but in this family they are largely elongate, and of specialized form (see below). The anomalous hemiacridine acridid, *Pyrgacris* has very similar structures to those of some *Pyrgomorphidae* (Descamps, 1968). It is conceivable that these structures represent the styli of the epiphallus found in *Turanogryllus (Grylloidea)* disccussed by Randell (1964).

The plate-like or shield-like epiphalli figured by Dirsh (1956: pl. 3, figs. 4, 5, 6, 9) may all be derived from the bridgelike form through an increase in the size of the bridge itself, or of the lateral plates, or of both. The only significant difference in these forms is the absence of lophi. The *Acridoidea,* therefore, can best be separated into those with and those without epiphallic lophi. *Pyrgomorphidae* belong to the former group (see below).

The epiphallus in *Pyrgomorphidae* (Fig. 1, *B*) shows some departure from the generalized form. It is attached towards its distal and lateral connections with the dorsum of the cingulum or by the ectophallic membrane and the pallium respectively. The lateral plates (LP) are firmly joined at their bases to the lateral margins of the bridge (B). The former are most frequently braced by strongly sclerotized ridges running almost in an anteroposterior direction, and the latter is armed with small spinous processes (more prominent and widely distributed spines are found in *Pamphagidae* and *Trigonopterygidae).* The lateral plates may also have externolateral expansions to a varying degree, most clearly exhibited by the subtribe *Pyrgomorphina* (as defined by Kevan and Akbar, 1964), but also by such tribes as the *Chrotogonini* and *Taphronotini.* The anterior projections (AP) vary from small, broadly rounded lobes, sometimes slightly constricted basally, to elongate, slender processes (e. g. *Fijipyrgini* and some *Nereniini).* They are virtually absent in a few species, e. g. of *Phymateus, s. str.,* and *Acanthopyrgus.* The posterior projections are lacking as such, although the externolateral expansions of the lateral plates, referred to above, are probably homologous with them. In *Pseudomorphacris* there are posterior processes associated with the lophi, but these may not be homologous.

A pair of hook-like processes (L), termed posterior projections by Dirsh (1956), are situated at the posterior end of the lateral plates.

The form of these processes strongly suggests that their function is similar to that of the lophi of other *Acridoidea,* and the structures are now regarded as being, in fact, homologous with the lophi by Dirsh (1959, 1961, 1963 b, 1965), Kevan and Akbar (1963, 1964), Kevan (1964 a), Kevan, Akbar and Singh (1964), Kevan, Singh and Akbar (1964 a, b), Akbar (1966 a, b), Descamps and Wintrebert (1966 b) and others. The lophi of *Pyrgomorphidae,* unlike those of most other *Acridoidea* are borne by the lateral plates alone and not by the bridge of the epiphallus. *Lentulidae, Tristirinae* (= *Chilacridinae),* and some hemiacridine *Acrididae,* e. g. *Tarbaleus, Pyrgacris* (Kevan, 1966 g; Descamps, 1968), have similary placed lophi. They are upwardly curved, but their apices may be directed laterally, anteriorly or anterolaterally. The apices are strongly acute in most *Pyrgomorphidae,* but in a few they may be obtuse of truncated. In *Atractomorpha* and *Occidentosphena* they are lobe-like. In *Brunniella,* elongated and externally denticulate; and in *Pseudomorphacris,* bifid. Ancorae are always absent in *Pyrgomorphidae* [7]. These are the anterior 'uncinietti' or 'unguiculae penis' of Berlese (1882), or 'apophyses en virgale' of Peytoureau (1895).

Attached marginally or submarginally on or near the anterior projections (Fig. 1 *B,* AP) of the lateral plates (LP) is a pair of elongated, usually club-shaped structures (A[OS]) — the "dorsolateral appendices" of Dirsh (1956). Both Roberts (1941) and Dirsh *(l. c.)* indicated that these may be homologous with the oval sclerites of other *Acridoidea* (see above). Eades *(in litt.,* 1962) deduced from his studies of the musculature of *Atractomorpha* that this is definitely the case; Kevan and Akbar (1964), Kevan (1966 g) and Akbar (1966 a, b) so regard them. For the sake of uniformity, the term "appendices" (without the cumbersome epithet "dorso-lateral") is adopted here for all *Acridoidea* in which the structures occur, because the word 'oval' is inapplicable to *Pyrgomorphidae* and scarcely more appropriate for many other *Acridoidea* (Akbar, 1966 b).

The epiphalli of a few genera of *Pyrgomorphidae* are strongly modified (e. g. *Fijipyrgus, Ichthyotettix, Modernacris, Verdulia, Brunniella, Pseudomorphacris, Occidentosphena* and *Atractomorpha),* but, in all, they conform to the same basic pattern which is diagnostic for the family.

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[7] Dirsh (1959, 1963 b) states that they are present in *Chapmanacris* and *Pyrgohippus,* but the processes involved are, in fact, merely parts of the anterior projections of the lateral plates.

d) *The Ectophallus.*

Ectophallic membranes and the cingulum as a whole. In its simplest, though not necessarily most primitive, form (most *Eumastacidae, Eumastacoidea)* the ectophallus is a membranous, or weakly sclerotized, sac-like or capsule-like structure (Dirsh, 1956, 1961, 1964 b; Rehn and Grant, 1958; Descamps, 1964). There is no cingulum even when sclerotization is heavier *(Episactinae).* A simple type of cingulum is found in the eumastacoid *Proscopiidae* and in *Pneumoroidea* (Dirsh, 1956, 1961), as well as in *Tanaoceroidea* (Rehn and Grant, 1958), but in *Acridoidea,* only the *Xyronotidae* (removed to *Pneumoroidea* by Dirsh (1966 b)) have a reduced cingulum representing the zygoma and apodemes of other families (Kevan, 1952 a). In other *Acridoidea* the ectophallus is clearly differentiated into ectophallic membrane and sclerotized cingulum The latter, according to Randell (1964) is probably homologous with the rami of the *Grylloidea,* although it may well be that the homology extends little further than to the similarly named parts of the cingulum. In the *Acridoidea,* a well defined and sclerotized cingulum is considered to represent the more 'primitive' condition. Derived forms may be either highly specialized (as in *Pyrgomorphidae)* or degenerate (as in *Xyronotidae).*

The ectophallic membrane (Fig. 1, *C, D,* EM) is composed of two layers: an inner, thin, and an outer, thick, membrane (Akbar, 1966 b). These partly or completely enclose the phallic organs. The inner layer is joined to the zygoma (Z) and rami (RC) and extends to the distal dorsal part of the cingulum. In this region it becomes reflexed to form the basal fold (BF). The outer ectophallic membrane runs anterodorsally as far as the epiphallus. The mesal and lateral parts of the membrane are attached to the posterior margins of the epiphallic bridge and lateral plates. The outer and inner layers of the ectophallic membrane extend laterally on either side of the cingulum to form lateral lobes (Fig. 1, *C,* LL), which are joined with the rami (RC). Sometimes the lateral lobes join ventrally to form a ventral lobe *(Ommexechidae* and most *Acrididae).* The ectophallic membrane may also develop a thin pouch-like invagination, the ventral infold (Fig. 1, *D,* VI), which covers the anteroventral part of the cingulum.

The cingulum of *Acridoidea, sensu stricto,* (except *Xyronotidae,* see above) is a strongly sclerotized structure, that of the *Pyrgomor-*

phidae showing much more variation than in other families. Typically in most *Acridoidea,* it is composed of a pair of strongly sclerotized, rod-like or lobe-like apodemes (Fig. 1, *C,* AC) joined at their bases by a narrow, transverse, strap-like zygoma (Z). The latter is connected to a pair of dorsal, sometimes ventral, aedeagal valves. Sometimes a small sclerite, the arch of cingulum (CA) is joined to the zygoma (Dirsh, 1956). The zygoma, or the arch, according to Dirsh *(l. c.)* may bear a pair of cingulum valves (CV) — the dorsal valves of the aedeagus of Snodgrass (1935 b) and Roberts (1941). The rami of the cingulum (RC) extend laterally and ventrally from the zygoma, either remaining separate or becoming fused in the midventral part of the cingulum. Eades (1962) observed that "the rami of the cingulum in a broad sense include two pairs of processes, not just one". He accordingly restricted the term 'rami' to the much larger ventral pair and designated the dorsal, usually much smaller, pair as 'suprarami'. The rami may be excised ventrally and, together with the endophallic membrane, form a slit-like opening, the ventral cleft (Fig. 1, *D,* CV), which may extend dorsally between the valves of the cingulum.

The ectophallic membrane of *Pyrgomorphidae* does not deviate greatly from the generalized condition. The inner layer (Fig. 1, *D,* EM) is attached usually to a suprazygomal plate (SZ), or, rarely, to the zygoma (Z), especially when the plate is weak. In some genera the basal fold (BF) extends beyond the suprarami (later designated SR in detailed figures of various genera) and encloses the valves of the cingulum (CV) and the 'aedeagus', whereas in the majority of cases the basal fold does not cover these parts. The lateral lobes (LL), however, are joined in the lateroventral parts of the rami and never form a ventral lobe. The inner layer of the lateral lobes extends anterolaterally and remains closely attached to what are here termed the apodemal plates (Fig. 1 *D,* AC — see also below), whereas the outer layer runs along the lateral extensions of the pallium; together they join with the appendices (A) of the epiphallus. The ventral infold (VI) is always present. From it develops the ventral process (VP), of varying shape and size (rarely vestigial), which is located in the anteroventral part of the cingulum. The outer layer of the ventral infold is continuous with the pallium (PL) ventrally.

The cingulum of *Pyrgomorphidae* is remarkably different from that of other families of *Acridoidea.* It is rather strongly sclerotized and capsule-like, entirely enveloping the endophallus. As an example of the

family, Roberts (1941) and Dirsh (1956) described the phallic structures of *Phymateus morbillosus* (Linnaeus) in which Roberts *(l. c.)* considered the various parts of the cingulum, namely zygoma, apodemes and rami, to be poorly differentiated. Dirsh *(l. c.)* named these areas only provisionally, because of their peculiar location and form, being doubtful "whether any parts of this cingulum are homologous with the parts of the cingulum of other families". That they are so, can now be seen from the anomalous hemiacridine, *Pyrgacris (Acrididae),* in which the dorsal aspect of the cingulum is distinctly pyrgomorphoid, although the rest is not (Descamps, 1968).

However, it would seem from the present study that, once the location and disposition of the zygoma is established, the parts of the cingulum in *Pyrgomorphidae* may indeed be homologized with those of the generalized acridoid. That part of the cingulum providing dorsal attachment for the inner layer of the ectophallic membrane corresponds to the zygoma of other forms and may be homologized with it (Fig. 1, *C, D,* Z). As in other families, apodemelike structures (AC) extend forwards from the zygoma, but instead of being rod-like or rather narrow, flat structures (Fig. 1, *C),* they are expanded anterolaterally and are large and lobe-like in form (Fig. 1, *D*); they do not appear to be fully homologous with the ectophallic apodemes of other families (see below). In *Pyrgomorphidae,* the rami (not shown in Fig. 1, *D*), which run backwards from the zygoma, are also large, extending at their posterior ends into the large posterior lobes of the cingulum which together usually form a so-called 'sheath' for the apex of the endophallus. In the present work the extension of each ramus is individually termed a 'sheath of the ectophallus' (later designated S in the illustrations of the various genera). Further, the term 'cingulum' is here restricted to the sclerotized parts of the ectophallus and thus usually includes only parts of the sheaths. It does not include the mid-dorsal membranous area lying between the rami and zygoma; this is the 'central membrane of the ectophallus' (see Fig. 1, *D,* CM, and p. 250).

Zygoma and associated structures. The zygoma was defined by Snodgrass (1935 b), without using the term cingulum, merely as a strong, transverse, sclerotic bridge of the ectophallus, and it has been variously interpreted subsequently. When Roberts (1941) referred to the cingulum of *Acridoidea* as a "collar-like" structure, he applied various terms, including 'apodemes', 'rami' and 'zygoma', in a largely topo-

logical sense, to its parts. He defined the zygoma as "the median transverse part of the cingulum which lies under the caudal part of the basal fold". Dirsh (1956) defined the zygoma somewhat similarly, indicating, however, that he did not consider it to be a separate sclerite. Hubbell (1960) regarded the mid-dorsal membranous area associated with the zygoma as being part of the cingulum, naming it the "basal eminence" or the "summit of the zygoma", thus implying that the zygoma included this area. Eades (1961 b) also maintained that the definitions of the "arch of the cingulum" given by Roberts and Dirsh *(ll. cc.)* indicated that these authors similarly mean by 'zygoma' the entire mid-dorsal region, sclerotized or otherwise. Eades, himself, however, considered the membranous area to be separate from the zygoma, although he recognized it as being part of the cingulum, proposing for it the term "central membrane of the cingulum".

In the present work, as previously, we follow Eades (1961 b) in considering that the membranous area should not be regarded as being truly part of the zygoma, but, further, we now prefer to regard it as being distinct from the cingulum proper also, at least until such time as it can be demonstrated that the two have a common derivation. Kevan and Akbar (1964), for this reason, called it the "central membrane of the ectophallus", althought it was designated "membrane of the cingulum" by Kevan (1964 b) and "central membrane of the cingulum" by Kevan (1966 b).

The zygoma in *Pyrgomorphidae* may be wide (in *Pyrgomorphella,* for exemple) and may even occupy almost the entire dorsum (e. g. in *Gymnohippini).* Conversely it may sometimes be narrow and confined to the anterodorsal region (especially in *Nereniini,* but also, for example, in most *Orthacridini).* The extent of the central membrane (Fig. 1, *D,* CM) thus varies greatly, occupying almost the whole dorsum in *Nereniini,* but being very small in *Ichthiacridini.* The zygoma also gives rise at its anterior end to a broad, overlying sclerite, the suprazygomal plate (SZ) — the 'dorsal process' of Dirsh (1956) — from the distal margin of which extends the inner ectophallic membrane (EM). A small, transverse, usually quite heavily sclerotized structure, designated the 'pseudoarch' (PZ) and defined by Akbar (1966 b), is present in the distal part of the central membrane, close to the bases of the suprarami (which are not shown in fig. 1). This bears the paired valves of the cingulum (CV) and serves to join the cingulum to the dorsal part of the endophallus.

Apodemal plates and rami. The apodeme-like lobes in *Pyrgomorphidae* normally extend anteroventrally from the zygoma, forming broad, externally convex plates with rounded anterior margins (Fig. 1, *D,* AC). The lobes are, however, narrower and apically pointed (when seen in lateral view) in a few genera (notably in *Verdulia),* or have small, downwardly-directed anterior projections or 'ventral processes' in a number of others (particularly in *Orthacridini).* The muscle attachments suggest that only the ventral processes should properly be regarded as being homologous vestiges of the ectophallic apodemes of other *Acridoidea,* whereas the large lobes with which they are continuous should be interpreted differently, although it is not certain how. The latter have, therefore, been termed 'apodemal plates' by Kevan and Akbar (1964), although Akbar (1966 b) and Kevan (1966 g) retain 'apodemes of cingulum'.

The rami of the cingulum in *Pyrgomorphidae* are basically similar to those of other families (Fig. 1, *C,* RC), and, in most instances, each is similarly divisible into a smaller dorsal process, the supraramus (later designated SR in the detailed figures for the various genera), and a large, ventral part, the true ramus (RC). In some genera, however, suprarami are indistinct. The rami always contribute to the formation of the ventral cleft (Fig. 1, *D,* VC), when this is distinct, and usually extend into the sheaths (S in the detailed figures), except occasionally when the latter are lacking.

Reinforcing structures. Seen in dorsal view, the anterior margin of the cingulum is usually strongly emarginate (the basal emargination), and this region is generally somewhat more heavily sclerotized than adjacent areas. It has been termed the 'basal thickening' (later designated BC in the figures for the various genera). Its main function would seem to be strengthen the cingulum, and it extends on either side around the edges of the apodemal plates and thence along the ventral regions of the cingulum as a pair of longitudinal thickenings. Each may be continued along the corresponding ramus as far as the endophallic extension to the cingulum. Sometimes ventral and lateral oblique thickenings also strengthen the cingulum, while the ventral longitudinal thickenings usually give rise to a further ventral transverse thickening at the base of the ventral process (Fig. 1, *D,* VP); this is often incomplete. The various areas of sclerotization will be indicated in the detailed figures for the various genera and designated VOC, LOC, VLC and VTC respectively.

Valves of cingulum. Roberts (1941) considered what he called the arch of the dorsal valves to be developed from the "aedeagal valves" or the endophallic membrane. Dirsh (1956), on the other hand, believed the arch and the valves of the cingulum (the latter corresponding to Roberts' dorsal valves) to be "morphologically derived from the ectophallus". Eades (1961 b) states that Dirsh's concept "would require that the ventral portion of the phallotreme is endophallic and dorsal portion ectophallic, or else that a diverticulum develops from the ectophallic membrane, grows down what is to be the arch, and expands to form the dorsal aedeagal sclerites, which fuse with the phallotreme membrane". He indicates that the arch and dorsal aedeagal sclerites do not establish a sclerotic connection with the cingulum, but in many instances form a continous sclerite. Eades *(l. c.)* also suggests that the valves of the cingulum in *Charilaidae* [= *Pamphagodidae*], and *Pyrgomorphidae* (as well as of the eumastacoid *Proscopiidae)* may show possible homology with the dorsal aedeagal sclerites, but that "such a homology would be dubious on anatomical grounds alone".

In *Pyrgomorphidae* the valves of the cingulum (Fig. 1, *D,* CV) originate from the pseudoarch (PZ) and are, therefore, ectophallic in origin. Moreover, they do not participate in the formation of the phallotreme, their chief function being auxillary rather than accessory. These valves, therefore, do not correspond functionally to the "dorsal aedeagal valves" of other *Acridoidea.* In form they are very variable both in size and complexity; frequently they are beset with minute denticulations. They are particularly large and complex in *Ichthyotettix* and *Pseudogeloius,* but they are usually rather small and may even be virtually absent.

e) *The Endophallus.*

The endophallus of *Acridoidea* is derived from the endophallic sac which differentiates into spermatophore sac, ejaculatory sac and endophallic sclerites. The latter are composed of proximal expanded plates, the endophallic apodemes (Fig. 1, *C,* EA), and the distal elongated rod-like sclerites of the aedeagus (AE). The lateral plates (LT) — suggested by Randell (1964) to be homologous with the endoparameres of *Grylloidea* — form the median parts of the endophallic sclerites and lie against the spermatophore sac (SS). A pair of gonopore

processes (GP), which arise from the ventral part of the endophallic apodemes partly separate the spermatophore sac from the ejaculatory sac (ES), and mark the position of the (primary) gonopore (G).

According to Dirsh (1956, 1961) the aedeagal sclerites of *Acridoidea (sensu lato)* are of five types (of which the first two are, in fact, found only in *Eumastacoidea,* not in *Acridoidea, s. str.)* (1): a single rod-like sclerite *(Proscopiidae);* (2) a single sclerite forming an arch *(Eumastacidae)* [8]; (3) a pair of rod-like sclerites ([most] *Pyrgomorphidae* and *Lentulidae);* (4) a pair of sclerites, each divided into basal and apical parts, which, however, are connected by a flexure (Fig. 1, *C,* FX) *(Ommexechidae* and *Acrididae);* and (5) a pair of sclerites, each member of which is completely divided into basal and apical parts *(Trigonopterygidae, Charilaidae* [= *Pamphagodidae*], *Pamphagidae, Lathiceridae* and *Pauliniidae).* The last type is believed by the present authors to represent the basic (or 'primitive') condition in *Acridoidea;* types 4 and 5 are both found in a few *Pyrgomorphidae* (Kevan and Akbar, 1964), although this was not known to Dirsh *(ll. cc.).*

The spermatophore sac (SS) may be located dorsally, ventrally, or partly between the aedeagal sclerites; the ejaculatory sac (ES) lies ventral to, or between them. The two sacs communicate with each other through the primary gonopore (G). The spermatophore sac extends as a narrow phallotreme duct (Fig. 1, *D,* PD — phallotreme of most authors, in part) as far as the apical aedeagal opening, the true phallotreme or secondary gonopore (this is not shown in Fig. 1). Sometimes the aedeagal sclerites are not connected ventrally by the membrane. The aedeagal opening (phallotreme) in such cases is in the form of a vertical slit which is continuous with the ventral opening of the ejaculatory sac.

The endophallus of *Pyrgomorphidae* (Fig. 1, *D*) is a comparatively simple paired structure. Each endophallic sclerite comprises an anterior, flared, endophallic apodeme (EA) whose walls may be either laterally compressed at the base or dorsoventrally flattened, and a distal, usually curved and tapered, rodlike aedeagal sclerite (AS). Sometimes the endophallic apodemes form dorsal inflections which may

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[8] The single (median) aedeagal sclerite is presumably derived by fusion of paired structures (Randell, 1964), or it must be non-homologous with the paired aedeagal sclerites of the *Acridoidea, s. str.*

cover the basal part of the spermatophore sac (this is very exaggerated in *Modernacris* and *Apodesmoptera)*. The aedeagal sclerites are normally undivided at their apices, although in *Fijipyrgini, Mitricephalini, Geloiini* and *Tagastini* the apices are separated off as small individual sclerites (in the detailed illustrations of the relevant genera these are later designated AS_2; the body of the aedeagal sclerite AS_1). The apices of the aedeagal sclerites are enveloped by the aedeagal valves (Fig. 1, *D,* AV), which are partly ecto- and partly endophallic in origin. Occasionally, as in some *Orthacridini* and *Ichthiacridini,* the apices of the aedeagal valves may be constricted or marked off by a weakly sclerotized connection.

Roberts (1941) and Dirsh (1956) do not clearly differentiate between the aedeagal sclerites and the aedeagal valves, to which they refer rather loosely, but Eades (1961 a, b) distinguishes between the solidly sclerotized parts of the endophallus — aedeagal sclerites — and the thinner, enveloping, terminal parts — the aedeagal valves. In *Pyrgomorphidae,* the paired nature of the valves is not always obvious, and they often appear to form a single sheathlike structure. The form of the valves is rather variable. In *Verduliini,* for example, they may be very large and sleeve-like, and in *Desmopterini* they are often cap-like; they are frequently beset with minute denticulations.

The lateral plates of the endophallic sclerites, found in the generalized Acridoid (Fig. 1, *C,* LT), and an identifiable gonopore processes (GP) are lacking in all *Pyrgomorphidae,* the former having probably combined with the aedeagal apodemes (Fig. 1, *D,* EA). In this family, the spermatophore sac (SS) lies dorsal to the aedeagal sclerites (AS) and distally forms the phallotreme duct (PD). The ejaculatory sac (ES) occupies a ventral position. The spermatophore sac and ejaculatory sac communicate with one another through a transverse, slit-like connection lying dorsal to the aedeagal sclerites, which marks the position of the primary, or true, gonopore (G). The phallotreme duct connects the left and right aedeagal sclerites, although a ventral union is lacking, so that the phallotreme (not shown in Fig. 1, but later indicated by P in the illustrations for the various genera), instead of being terminal, forms a slit-like ventral opening. The phallotreme is continuous with the ventral opening of the ejaculatory sac which, along with the fused endo- and ectophallic membranes, joins the rami and sheaths of the ectophallus to form the ventral and dorsal clefts, respectively.

Roberts (1941) distinguished two principal conditions occurring in acridoid endophalli: the ejaculatory sac either closed *(Cryptosacci)* or open as in *Pyrgomorphidae (Chasmosacci)*. Dirsh (1956) rejected Roberts' concept of two groups based upon this criterion, and maintained that the ventral slit, in the latter group, which Roberts believed to be the opening of the ejaculatory sac, is "actually the ventral part of the opening of the phallotreme". However, as already noted, the ventral slit-like opening of the phallotreme and the opening of the ejaculatory sac are confluent and together form the ventral cleft. Eades (1962) has indicated the possibility that in chilacridine *Acrididae* [= *Tristirinae*], *Pyrgomorphidae* and *Lentulidae,* the so-called aedeagal sclerites are actually enlarged gonopore processes which "serve as the division between the spermatophore sac and ejaculatory sac". In *Pyrgomorphidae* and *Lentulidae,* according to him, it would be the true aedeagal sclerites (not the gonopore processes), as well as the lateral plates, that are absent, so that the spermatophore sac comes to occupy a dorsal position, whilst the ejaculatory sac opens directly into the genital chamber.

In those tribes of *Pyrgomorphidae* in which the aedeagal sclerites are divided, the elongate basal pieces (which are continuous with the aedeagal apodemes) would, according to the concept of Eades (1962), represent the gonopore process, and the distal parts could be regarded as remnants of the true aedeagal sclerites. However, the investment of both the apical sclerites and the distal parts of the principal aedeagal sclerites by the same aedeagal valves renders Eades' view untenable. It is more probable in such *Pyrgomorphidae,* that the division into two parts of the endophallic sclerites represents the primitive condition. In a few genera (e. g. *Pseudogeloius)* the separation of the apical sclerites does not seem to be quite complete, and there is something resembling a flexure between the two parts, similar to what is found in *Acrididae;* in others *(Ichthiacridini)* there is merely a subapical constriction.

As the divided type of aedeagal sclerite is found in several families from widely scattered geographical areas — *Trigonopterygidae, Pamphagidae, Pamphagodidae, Lathiceridae* and *Pauliniidae* — all of which (except possibly the last) probably became separated from the main acridoid stock at an early date, it would seem that those *Pyrgomorphidae* with a similar structure are the most primitive so far as this character is concerned. In support of this view, it may be noted that,

although most *Pyrgomorphidae* have undivided aedeagal sclerites, those in which these are divided, or at least constricted, are also found in widely separated regions and may show little close relationship in other respects. It seems less likely that the aedeagal sclerites have become divided (or have acquired an additional appendix) several times over, both within and without the *Pyrgomorphidae,* than that of majority of that family have lost the additional sclerite (or that it has become fused with the principal sclerite) and that the same trend has occurred in *Acrididae.* Against this view, it should be noted that *Pyrgomorphidae* with divided aedeagal sclerites may also have very complex copulatory organs *(Mitricephalini, Fijipyrgini, Geloiini),* so that the division of the aedeagal sclerites might merely be a manifestation of this complexity. However, others do not *(Tagastini);* nor do all *Pyrgomorphidae* with complex genitalia have divided aedeagal sclerites (some *Nereniini* and *Ichthyotettigini).*

f) *Synopsis of the Phallic Characters of the Pyrgomorphidae.*

A very brief summary of the phallic characters of the *Pyrgomorphidae* was included in the definition of the family given by Kevan and Akbar (1964). The following expansion of this summary attempts to synthesize the characters of all the genera studied.

Epiphallus: bridge narrow to wide, its anterior and posterior margins with or, more often, without median processes; ancorae always absent; lateral plates posteriorly directed, sometimes obliquely so, externolateral expansions absent (usually) or of varying degrees of development; anterior projections typically lobelike, often constricted basally, sometimes pointed or narrow, occasionally very elongate, rarely absent; lophi arising directly from the lateral plates, with acute, subacute, rarely truncated or lobe-like apices, which are upwardly curved and directed laterally, anterolaterally or anteriorly; appendices usually club-shaped, with stout to slender stalks attached submarginally or marginally to the posterior parts of the anterior projections or to the lateral plates, usually diverging from the latter, although sometimes closely applied to them, ending in narrow to broad apical lobes which may bear terminal processes, terminal parts of appendices usually reaching as far backwards as the bases of the lophi or falling somewhat short of these, occasionally much longer.

Ectophallus: ectophallic membrane with, or occasionally without, a basal fold covering the 'aedeagus'; lateral lobes simple or bilobed, small to large, occasionally somewhat sclerotized; ventral infold sometimes extending beyond the base of the cingulum, but not usually so; ventral process rarely absent, normally triangular or subtriangular, occasionally subtruncate or elongate, extending forwards for a variable distance, occasionally even beyond the base of the cingulum; central membrane very variable in extent, sometimes restricted to the laterodorsal parts of the cingulum, sometimes occupying almost the whole of the dorsum of the cingulum, rarely reduced to virtually nothing; cingulum proper capsule-like, basal emargination of variable width and depth, usually broadly U- or V-shaped, occasionally very small; basal thickening forming a margin to the basal emargination, narrow to plate-like; ventral longitudinal, ventral oblique, lateral oblique and ventral transverse thickenings variously present; apodemal plates broad but of variable width, occasionally produced into points anteriorly but more usually rounded, sometimes with small, anterior ventral processes (? true endophallic apodemes); zygoma plate-like, usually broadly rounded, sometimes covering the entire dorsum of the cingulum, occasionally reduced; suprazygomal plate, when present, usually with a rounded, or occasionally a truncated, apex, generally smaller, rarely larger, than the zygoma; valves of cingulum usually present, finger-like and smooth, or platelike or lobed and often denticulate; pseudoarch, if present, short and broad (usually forming an inflection dorsally) to long and slender (without inflection); rami large, excised ventrally, sometimes extended to form external flap-like 'inflections', rarely forming internal inflected processes; sheaths small to large, rarely absent; dorsal cleft present or not; ventral cleft small to large, occasionally virtually absent.

Endophallus: endophallic apodemes laterally compressed or sometimes dorsoventrally flattened, often with dorsal inflections; the latter, when present, sometimes covering part (occasionally much) of the spermatophore sac; aedeagal sclerites of variable length and stoutness, occasionally very slender and greatly elongated, usually upwardly curved apically, sometimes straight or sinuous, rarely decurved, apices acute or subacute, rarely truncated, usually composed of single, undivided sclerites, but sometimes divided so as to form long basal and short apical parts, the distal parts either quite separate or joined by a flexure; aedeagal valves usually weakly sclerotized, almost always enveloping

the entire posterior ends of the aedeagal sclerites, the latter only rarely protruding beyond the valves; aedeagal valves of variable length and form, generally, but not always, longest and most slender in genera with slender, elongate aedeagal sclerites, usually conical with acute or subacute apices, sometimes truncate, sleeve-like, cap-like or of irregular shape, often minutely denticulate, sometimes with apical parts marked off from the rest by a constriction or membranous region; spermatophore sac spherical, subspherical, longitudinally ovoid or transversely elliptical, rarely with a distal, dorsal diverticulum; gonopore transverse, basal, mesal or distal in position; ejaculatory sac varying in size from small to large, but almost invariably simple in form.

4. The acridoid female subgenital and spermathecal structures, with special reference to the Pyrgomorphidae.

a) *General Remarks.*

The female abdominal terminalia of *Acridoidea* have been the subject of investigation by numerous authors over many years. Some of these investigations have been of a general anatomical nature; others restricted to a few species. It is not, however, appropriate here to review all the literature, because much of it concerns the ovipositor and associated structures with which the present study is not concerned.

The earliest contributions are reviewed in the major works of Peytoureau (1895) and Chopard (1920). The following authors, in chronological order, are among those that have been consulted in the present context. Brunner von Wattenwyl (1876), Packard (1878), Berlese (1882), Peytoureau (1895), Fenard (1896), Comstock and Kellogg (1899), Berlese (1908), Walker (1919), Chopard (1920), MacGillivray (1923), Sokolow (1926), Fedorov (1927), Boldȳrev (1929), Nel (1929), Vardé (1929), Weber (1933), Vardé (1934), Guarino (1935), Snodgrass (1935 a, b), Slifer and King (1936), Paoli (1937), Jannone (1939), Slifer (1939), Qadri (1940), Slifer (1940 a-c), Karandikar (1942), Slifer (1943 a), Chopard (1949), Voy (1949), Gupta (1950), Agarwala (1952 a, b), Kevan (1952 a), Albrecht (1953), Agarwala (1953, 1954), Beier (1955), Albrecht (1956), Ander (1956), Katiyar (1956), Dirsh (1957), Lux (1957), Kevan (1959), Mika (1959), Rehn and Grant (1959 a-c, 1960 a-c), Lux (1961), Uvarov and Dirsh

(1961), Márquez Mayaudón (1967), Eades (1962), Dirsh (1963 a, b), Randell (1963), Rehn and Randell (1963), Thomas (1963), Vickery (1964), Gregory (1965), Descamps (1966), Descamps and Wintrebert (1966 b), Akbar (1966 a), Kevan (1966 a-c, e-g, 1967 a), Uvarov (1966), Vickery (1967 a, b) and several others received subsequent to going to press. Some of these authors concern themselves primarily with morphology; others with taxonomy. The works of Slifer (1940 b), Dirsh (1963 b), Randell (1963), Akbar (1966 a) and Kevan (1966 a, b, e-g, 1967 a) bear most directly upon the present study. Of the others mentioned above, only Chopard (1920), Nel (1929), Agarwala (1952 b, 1953, 1954), Katiyar (1956), Dirsh (1957), Kevan (1959), Márquez Mayaudón (1967) and Descamps and Wintrebert (1966) refer to *Pyrgomorphidae*. One or two brief, additional references to pyrgomorphid female structures have been omitted for the present.

Although previous authors have achieved some degree of uniformity of terminology for the ovipositor and associated parts, there has been little attempt to standardize that used for subgenital and spermathecal structures. Some attempt is made here to rationalize the use of terms and to eliminate certain ambiguities. This has unfortunately led to the discarding of one or two rather widely used terms. Definitions of those used in the present study will be found in the glossary, pp. 240-248).

b) *The Subgenital Armature.*

General. Since the term 'egg-guide' was introduced by Packard (1878) for the median terminal process of the eighth abdominal sternum (or subgenital plate) of *Melanoplus (Acrididae)*, this structure has been so named (or a translation used) by the majority of authors who have subsequently mentioned it. A number of other terms have also been used (see p. 242), but there has been no ambiguity regarding the structure referred to, except in the case of Sokolow (1926) who used the term 'subgenitale Platte' or 'Subgenitalplatte' for the egg-guide alone and not for the entire eighth sternum. The main function of the egg-guide has always been asumed to be to facilitate the passage of the eggs from the oviduct, which opens into the genital chamber, to a position between the bases of the ovipositor valves. To this end it may be grooved on its dorsal surface, although this is not the case in all *Pyrgo-*

morphidae. Akbar (1966 a) considers that the egg-guide is accessory in function and that the true guiding structure is the 'ovitract' lying in front of it (see p. 194).

Although other subgenital structures in *Acrididae, s. str.,* have been indicated after a fashion, by one or two earlier authors, comparatively little attention has been paid to the dorsal side of the acridoid subgenital plate (i. e. the floor of the genital chamber) until quite recently. The earliest illustration seems to be that given for *Locusta* [as *Oedipoda*] *migratoria* Linnaeus by Berlese (1882), without detail or comment. Peytoureau (1895) also illustrated the upper surface of the eighth sternum for *Dociostaurus* [as *Stauroderus*] *maroccanus* (Thunberg) and referred briefly and rather vaguely to some of the parts. Chopard (1920) gave a sketch for *Anacridium* [as *Orthacanthacris*] *aegyptium* (Linnaeus), without detail; Sokolow (1926), for *Locusta,* showed slightly more, but interpreted very little of his drawing. Nel (1929) refers to 'secondary pockets' or 'lateral pouches' at the base of the egg-guide in *Locustana* [*pardalina* (Walker)] *(Acrididae)* and, by implication, *Colemania sphenarioides* Bolívar *(Pyrgomorphidae),* illustrating them in cross-section for the immature stages of the former species; again no comment is made.

Several authors (Peytoureau, 1895; Comstock and Kellogg, 1899; MacGillivray, 1923; Vardé, 1929, 1934; Snodgrass, 1935 b; Slifer and King, 1936; Slifer, 1939, 1940 a, 1943 a, Karandikar, 1942, and others later) have referred, by different names, to pocket-like, glandular pouches in the anterior part of the genital chamber of certain *Acrididae,* but these do not appear to be the same as the pouches mentioned by Nel (1929), although they do seem to be the 'lateral pouches of the gynatrium' of Gupta (1950). They have come to be known as Comstock-Kellogg glands. They do not occur in *Pyrgomorphidae* (Vardé, 1934 [implied only]; Slifer and King, 1936; Slifer, 1940 a); nor are they regarded as constituting part of the subgenital armature, and they are of no further concern here.

Peytoureau (1895) differentiated certain parts of the female subgenital armature in *Dociostaurus maroccanus,* but it may be said that Jannone (1939) was really the first to publish anything of significance on the structures involved when he illustrated them in more detail for the same species. He did not, however, name the parts figured, other than the egg-guide. Karandikar (1942), who probably antedated Jannone, as his work on *Schistocerca gregaria* (Forskål) was more than

a decade old when it was published, was more through in his treatment and used a loose terminology for several of the structures he observed. When Agarwala (1952 a, b, 1954) discussed the subgenital plate for a number of *Acridoidea,* he introduced different terms for certain of the parts figured by Jannone *(l. c.* — see p. 194). Virtually no further advance was made until Randell (1963) published a reasonably comprehensive, although poorly documented, comparative account of the female subgenital structures, or "copulatory armature", of the *Orthoptera-Caelifera.* This author examined a small number of representatives of almost every family and subfamily of the group, but he unfortunately omitted reference to the works of Jannone, Karandikar and Agarwala *(ll. cc.),* so that his more extensive terminology was different again. His terms were, however, adopted by Kevan (1963) in describing the subgenital plate of *Kuantania aptera* Kevan and in subsequent works on *Pyrgomorphidae,* by Vickery (1964), with slight modifications, for the genus *Chorthippus (Acrididae),* and by Akbar (1966 a) for six genera of *Pyrgomorphidae.* Thomas (1963, 1965), in her morphological works on *Locusta* and *Schistocerca gregaria* (Acrididae), used a mixture of her own and Agarwala's terms. Descamps (1966) also used a mixture of terms for *Pamphagodes (Charilaidae* = *Pamphagodidae).*

Randell (1963), in his survey, concluded that the correlation between the various forms of epiphallus and certain types of "postvaginal sclerite" (see p. 193), together with the presence and relative prominence of the egg-guide, is morphologically very important. He emphasized that the form of the female armature could help to interpret the function of portions of the male genitalia, notably of the epiphallus. He also observed that the structure of the postvaginal sclerite in some subfamilies of *Acrididae* is of considerable taxonomic interest. It was, in fact, on the basis of this observation that Rehn and Randell (1963) used the subgenital armature as a specific character in *Melanoplini (Acrididae).* Vickery (1964, 1967 a, b) found that the structures were basically similar in several species of *Chorthippus* and other *Acrididae,* but that there were minor differences between them. Kevan (1966 a-c, e, g, 1967 a) has recently illustrated the subgenital armature for various genera of *Pyrgomorphidae* and *Trigonopterygidae,* and (1968 a) for *Pycnosarcus (Acrididae, Romaleinae).* He found that it provides useful taxonomic characters at the generic, and sometimes the specific level. One genus, *Spinacris,* known only from the female, was

transferred from the *Acrididae* to the *Pyrgomorphidae* largely because of this, its post-vaginal sclerite being of a highly specialized type characteristic of the tribe *Verduliini* (Kevan, 1966 b). Two subtribes of *Pyrgomorphini* may also be separated on the basis subgenital armature, as well as by other characters (Kevan, 1966 e). Thus the preliminary contention of Akbar (1966 a) that it is not possible to use the female copulatory armature for taxonomic purposes at the generic or tribal level is not alwaye tenable. Descamps and Wintrebert (1966 b) illustrate the subgenital armature for several species of *Pyrgomorphidae* and *Acrididae*. Outside the *Acridoidea,* Descamps (1964) and Blackith (1966 b) have figured the dorsal surface of the subgenital plate of several genera of *Eumastacoidea (Eumastacidae: Euschmidtiinae* and *Morabinae).*

Posterior margin. The most prominent feature of the subgenital armature in the *Acridoidea* is the egg-guide (see above), which is present in the vast majority of species (Fig. 2, *A,* EG). Its absence is, in fact, confined to a few anomalous families (Randell, 1963). In *Pyrgomorphidae* it is always present (except in *Brunniella* ?), but varies considerably in its prominence: very long and acute, for example, in *Chlorizeina;* short and blunt, or almost suppressed, in many *Desmopterini.* In some genera the egg-guide is provided with a mesal thickening or dorsal groove which assists in conducting the eggs to the ovipositor; in others (e. g. *Dictyophorini)* these features are lacking.

The greater part of the posterior margin of the subgenital plate is reflexed upwards and forwards to form the floor of the genital chamber (Peytoureau, 1895; Nel, 1929; Karandikar, 1947). The external margin itself (Fig. 2, *A,* PE) was termed "posterior edge" or "fused edge" by Agarwala (1952 a, b, 1954). The former term is preferred here because the latter — also "fusion edge" of Vickery (1964) — is not always appropriate; frequently, as in *Pyrgomorphidae,* there is little or no fusion between the parts. In many *Pyrgomorphidae* the posterior edge is crenulated or even serrated.

Floor of the genital chamber. This consists largely of a thin, sclerotized, but mostly unpigmented, layer (Fig. 2, *A,* PVS), called by Randell (1963) the "post-vaginal sclerite", or "post-vaginal sclerotic areas", according to degree of development. The former term has been adopted by subsequent authors and is here used for all conditions. Contrary to the assertion of Randell *(l. c.)* that this structure had not previously been referred to, it seems clear from his illustration that

what Peytoureau (1895) called "la lame bilobée" is, in fact, this sclerite; and Karandikar (1942) used the term "underfolded plates". In *Acridoidea* in which the epiphallus is plate-like or shield-like, the post-vaginal sclerite is also plate-like, but in the majority of *Acridoidea,* in which the epiphallus is bridge-like, the post-vaginal sclerite is divided into two, usually subcircular or semicircular, halves only narrowly connected in front of or above the base of the egg-guide, although, in some instances, the connection is severed. The *Pyrgomorphidae,* having a bridge-like epiphallus, conform to the general pattern, but there is much variation in the form of the sclerite.

Some *Pyrgomorphidae* have very characteristic post-vaginal sclerites. This is particularly true of *Verduliini* (see above) in which the plate is strongly reticulate or beset with numerous oblique sinuous ridges (Kevan, 1966 b); many *Desmopterini* and *Nereniini* have prominent, minutely denticulate areas (Kevan, 1966 a, b). These areas are probably analagous to the "contact areas" of Randell (1963) found in many *Acrididae* (Fig. 2, *A,* CA), which are more strongly sclerotized, often pigmented, patches on either side near the base of the egg-guide. These, too, are referred to by Peytoureau (1895) — as "parties centrales plus chitinisées". In those *Pyrgomorphidae* just mentioned, however, the denticulate areas may not be homologous with the contact areas of *Acrididae.*

Anterior to the post-vaginal sclerite, and partly covering it, is a pair of crescentic membranous invaginations (Fig. 2, *A,* FP), first mentioned by Peytoureau (1895), simply as a membrane, and later illustrated, but not discussed, by Chopard (1920), Sokolow (1926) and Nel (1929). Karandikar (1947) refers to them as the "intermediate membrane". Agarwala (1952 a, b, 1954) paid more attention to these structures and called them "floor pouches", the term adopted here. Randell (1963) referred to both pouches together as the "tunic", the name used by Rehn and Randell (1963), Kevan (1963, 1966 b), Vickery (1964) and Akbar (1966 a). Thomas (1963) simply called them "pockets", but later (Thomas, 1965) changed this to "lateral pouches" (a term actually used first by Nel (1929)). Between the pouches, in most *Acridoidea,* is a V-shaped 'ovitract' (Akbar, 1966 a) with a 'median longitudinal groove' (MLG), referred to, but not specifically named, by Agarwala (1952 b). The *Pyrgomorphidae* possess both floor pouches and ovitract, but they show little variation except in minor details of the form of the groove. According to Akbar (1966 a) the ovitract is

the principal structure guiding the eggs to the ovipositor, the so-called egg-guide being accessory. Mesally, immediately anterior to the floor pouches, is the female gonopore, vulva or vaginal opening of the common oviduct (V).

Boldȳrev (1929) suggests that the lophi of the male epiphallus are used to depress the floor or the female genital chambers (i. e. the post-vaginal sclerite) to expose the orifice of the spermathecal duct; this is implied also by Randell (1963) and Akbar (1966 a), although they do not refer to Boldȳrev. Randell relates the shape of the "contact areas" (see above) to the form of the lophi. Thomas (1965) considers that the floor pouches may act as a safety device, preventing the hook-like lophi from moving too far forward and damaging the internal structures of the female.

Columellae. Anterolaterally to the base of the egg-guide, there are, in the *Acrididae, Ommexechidae, Pamphagodidae* and many *Pyrgomorphidae,* but not in other families, small, paired, sclerotized connections between the post-vaginal sclerite and the dorsal surface of the subgenital plate proper (Fig. 2, *A,* C). These are indicated for several genera of *Acrididae* by Jannone (1936) and illustrated more clearly for *Dociostaurus* by the same author later (Jannone, 1939), but they are not named. Karandikar (1942), however, figuring them for *Schistocerca,* calls them "ridge-like outgrowths" or "elevations". In *Acrididae,* when distinct contact areas *(sensu* Randell, 1963) are present, these structures are associated, generally more or less centrally, with them. Randell *(l. c.)* calls them, "columellae" because of their vertical position and often rounded cross-section. The columellae may frequently also be of irregular outline, or composite, or sometimes multiple in nature, but they are never very large. Together with the surrounding "brown patches" (contact areas), they were termed "Jannone's organs" by Agarwala (1952 a) and they are also given this name by Thomas (1965) and Uvarov (1966). Agarwala's *(l. c.)* usage of his term, was, however, inconsistent; elsewhere in the same work and later (Agarwala 1952 b, 1954), only the columellae are indicated, or only the "brown patches" are referred to (Agarwala, 1954). Agarwala (1952 a: fig. 9) also mislabels as "Jannone's organs" what, in his text, he calls "Jannone's sensillae" (quite different structures), so that the former term is best avoided.

Both Jannone (1939) and Agarwala (1954) believed the structures discussed above to be sensory in function. Karandikar (1942), for

Schistocerca gregaria (Acrididae), regarded the columellae as sclerotized supporting structures, with which Agarwala (1952 a) concurred. Rehn and Randell (1963) considered the collumellae to be strengthening devices anchoring the post-vaginal sclerite, which would otherwise be permitted considerable freedom of movement. Several families of *Acridoidea,* and a large number of *Pyrgomorphidae,* however, are without columellae, so that any movement resulting from their absence cannot be of importance in these groups. Whether the columellae have any additional sensory function is unknown. Randell (1963) suggests that they are apparently of considerable importance in copulation, since the space between them varies in width to match the distance between the lophi of the epiphallus. In *Pyrgomorphidae,* however, this appears to hold good only for a minority of genera in which columellae are clearly developed, and then only if the bases and not the apices of the lophi are considered. Akbar (1966 a), in rejecting Randell's contention, found that, of the six genera he studied, only in *Poekilocerus* was there such a correlation, but his findings were inconclusive since he considered the apices of the lophi, which are directed outwards in all other genera, and not their bases. He also included under the term 'columellae' certain transverse or triangular thickened areas at the base of the egg-guide (found in four of the six genera, including *Poekilocerus),* which probabbly do not truly represent these organs (see below).

In most *Pyrgomorphidae,* columellae are either absent or reduced, although they may be prominent in many genera, e. g., in *Pyrgomorpha,* the only member of the family studied by Randell (1963). Their presence or absence does not seem to have any general phylogenetic significance within the family, although it might be assumed that, where columellae are absent, they have been lost, and that genera which possess them are more primitive in this respect. In the tribe *Pyrgomorphini,* the degree of development of columellae may vary considerably, but the subtribe *Pyrgomorphina* may be distinguished from the *Parasphenina* by possessing them (Kevan, 1966 e). In many tribes of *Pyrgomorphidae,* columella-like sclerotizations may be closely associated with the base of the egg-guide (see Akbar, 1966 a), and it is often difficult to determine whether or not reduced columellae are truly present. In this family, columellae are never composite or multiple — although they may sometimes be irregular in shape. They are not necessarily associated with contact areas; in fact, relatively few genera have both columellae and contact areas as in the *Acrididae.*

c) *The Receptaculum Seminis.*

Orthopteroid insects generally. The female organ that receives the spermatophore from the male has been variously termed 'receptaculum seminis' or 'spermatheca' (or a vernacular equivalent) in orthopteroid, as in other insects. The two terms are, in fact generally regarded as being synonymous (e. g. by Nel, 1929; Weber, 1953, Snodgrass, 1935 a; and many others). In the present work, however, the former is used for the whole organ, including its duct, whereas the term 'spermatheca' is reserved for the vesicular part or 'head' of the receptaculum without the duct or any diverticula associated with the latter. It might be argued that 'receptaculum' (a receiver or receptacle) and 'theca' (a vessel or cup) are indeed virtually synonymous, but some distinction is needed, and it is clear that if one term may be interpreted more widely than the other, it is 'receptaculum'. This course of action has been taken to avoid the confusion prevalent in the literature, in which one or other term (particularly 'spermatheca') has been used indiscriminately, inconsistently or ambiguously. Unfortunately Uvarov (1966), while as inconsistent in his usage as most other authors, in one place uses 'receptaculum seminis' in the restricted sense reserved here for 'spermatheca'.

The question of terminoloy is not altogether straightforward, for the organs acting as receptacula seminis may not necessarily be homologous in origin in all groups (Nel, 1929), although this is denied by Gupta (1950). However, in orthopteroid insects they are generally (if not always) derived in large measure from invaginations of the eighth abdominal sternum (Nel, Gupta, *ll. cc.)*. The situation is further complicated by the fact that, whereas in many orthopteroids the receptacula seminis are relatively simple, single structures, in others they may be paired. It would also seem that in many instances, partial fusion of structures has occurred, one member being subservient to the other, smaller in size and having a different function. In such instances the organ referred to as a (single) receptaculum, is compound. Several explanations for the compound receptaculum could be put forward. Perhaps the simplest (but the one for which there seems to be the least evidence in orthopteroid insects) is that it develops by dichotomy of a single median invagination of the eighth sternum. A second (for which there is considerable anatomical and phylogenetic,, but little

ontogenetic, evidence) is that the receptacula are primitively paired and that the left and right members of the pair have become united. A third explanation is that the receptaculum proper is of unpaired median origin and that the subsidiary part represents a median "accessory gland", developed from an invagination of the ninth sternum, and that this has moved forward to unite with the receptaculum proper (there is some anatomical and phylogenetic evidence for this also). Different explanations may apply to different groups. The presence of secondary diverticula on either the main receptaculum or its subsidiary, or on both, may further render homologies difficult to determine.

Snodgrass (1935 a), as had various authors before him (see Nel, 1929), expresses the view that receptacula seminis in insects generally may primitively have been paired, because of their double or bifurcate nature in many groups, not only in orthopteroids. Nel *(l. c.)* left the question open, although he himself had established separate origins for the paired receptacula in *Petrobius (Thysanura)*. [There is, however, a single receptaculum in *Lepisma*]. Snodgrass (1935 a), Beier (1955) and Dirsh (1957) have all mentioned that the bifid nature of the spermatheca usual in *Acridoidea* points to the probability of a paired primitive condition, although they did not enlarge on these views. Ander (1939) discussed the possibility a little more fully for *Ensifera*. Voy (1949) supported the idea of a paired origin in orthopteroids generally, suggesting that the left member was reduced to a lateral appendage or suppressed. Blackith & Blackith (1966 a) note that, in *Morabinae (Eumastacidae)* in which the spermathecal duct enters the bursa copulatrix laterally, it always does so from the right.

In the *Dictyoptera,* although the *Mantodea,* so far as is known, have but a single, simple receptaculum seminis, comprising a bulbous spermatheca and a relatively short duct, it has long been known that *Blattodea,* such as *Blatta* and *Periplaneta (Blattidae)* may have a bifid structure. This involves a primary (larger) and a secondary (smaller) reservoir [so termed by Voy (1949) following Fenard (1896)] or spermatheca, each having its own duct, the two uniting to form a short common duct. The secondary receptaculum, in fact, forms a lateral diverticulum of the primary one. All *Blattodea* are not alike, as has been demonstrated by various authors (e. g. Nel, 1929; Chopard, 1950; Gupta, 1950), but, recently, McKittrick (1964) has made a comprehensive comparative study, which has shown that in most *Blattodea,* other

than *Blattidae* and a few other small groups in which the bifid type occurs, the receptacula seminis are separate and paired (they may even be duplicated). In a few genera, however, only a single receptaculum occurs. In *Isoptera* this seems to be the general rule, but it is significant that in the primitive *Mastotermitidae* the bifid condition is found (McKittrick, *op. cit.)*. In *Phasmatodea* (see Beier, 1955) there may either be two simple, separate recurved receptacula (with a short common duct), as in *Diapheromera* (Marshall and Severin, 1906), or a single one as in *Carausius* (Nel, 1929). It would therefore seem that the paired, or at least forked, condition is the primitive one for orthopteroids other than *Saltatoria (Orthoptera, s. str.)* — even if the two receptacula develop initially from a single median invagination (Gupta, 1950).

The *Orthoptera s. str.,* also possess receptacula seminis that may be paired, bifid, or single. In the *Ensifera,* the great majority of, if not all, *Grylloidea (s. str.)* and *Tettigonioidea (s. str.)* have a single receptaculum without trace of a secondary reservoir, but in the *Gryllacridoidea,* which are in many ways more primitive, and apparently also in the *Schizodactyloidea,* the compound nature of the receptaculum may be demonstrated. Ander (1939) illustrates a series of conditions in *Raphidophoridae* ranging from that shown by *Ceuthophilus latens* Scudder, which has two short, similar, pouch-like receptacula, each with its own orifice, through that of *Troglophilus,* with two somewhat similar receptacula (the left of which is, however, reduced in size) opening through a short, common duct, to the form found in *Tachycines,* in which the two members differ greatly in size, the left one forming a vermicular lateral diverticulum opening into the common duct at a considerable distance from its orifice. This last condition is very similar to that found in *Blattidae,* although the common duct is longer and the 'secondary spermatheca' scarcely inflated. This situation, as will be discussed later, is paralleled in *Acridoidea.* As in *Acridoidea,* however, some genera of *Rhaphidophoridae* have only a single, simple receptaculum seminis. Ander *(l. c.)* also illustrates the receptaculum for a member of another family of *Gryllacridoidea,* namely *Stenopelmatus (Stenopelmatidae),* in which the secondary receptaculum has become reduced to a short, finger-like, lateral diverticulum arising from near the base of the spermatheca. In the *Schizodactyloidea (Schizodactylus, Schizodactylidae)* it would seem that this short, lateral diverticulum has become united with the spermatheca and has moved

still further upwards and even round its apex so as to lie 'head-downwards', as it were, on the opposite side of the spermatheca. These last two conditions are also paralleled in *Acridoidea* (including *Pyrgomorphidae*), as will be shown later.

Another interesting condition among the *Ensifera* is found in *Gryllotalpoidea (Gryllotalpidae)*. In *Gryllotalpa* (see, for example, Berlese, 1882; Fenard, 1896; Voy, 1949), as in true *Grylloidea*, there would appear to be no secondary receptaculum, but, from near the apex of the spermatheca, there arises a large, wide, U-shaped 'caecum', very reminiscent of similar structures found in many *Acridoidea*. This may be of considerable significance as the *Gryllotalpoidea* probably diverged from the *Grylloidea* at a very early date. At the end of the caecum, Berlese, Fenard and Voy *(ll. cc.)* show a narrow, finger-like process which could conceivably be the last vestige of a distantly migrated secondary receptaculum. A comparable condition is found in some *Pyrgomorphidae (Chrotogonini)*.

That the above parallels exist, not only within the *Orthoptera, s. str.*, between *Ensifera* and *Caelifera*, but also between *Orthoptera* and other orthopteroid orders (notably *Dictyoptera)*, would seem to provide fairly conclusive evidence for a similar origin for the compound type of receptaculum seminis in all groups, and could also point to a primitively paired origin, or at least forked condition, for the organ — although Gupta (1950) states (on the evidence of a few, far from primitive species only) that the receptaculum seminis "*always* develops as *a median invagination* of the eighth sternum" [our italics], even in *Blattodea* that have paired receptacula.

Against the hypothesis of a paired origin for the receptaculum seminis, however, it may be noted that in some *Orthoptera-Ensifera* (many *Tettigonioidea* and a number of *Gryllacridoidea)*, there is an unpaired, median, elongate, convoluted "ovipositor gland" (presumably an invagination of the ninth sternum), which is absent in the majority of *Orthoptera*. This is at least suggestive of the possibility that a compound receptaculum incorporates a displaced ovipositor gland and that the former is primitively unpaired. Unfortunately for this hypothesis, *Ensifera* with compound or paired receptacula may also have a well developed ovipositor gland (see Ander, 1939). In *Orthoptera-Caelifera*, only some *Tridactylidae* are known to have an ovipositor gland, and in this instance the receptaculum seminis is simple and unpaired (see below).

Caelifera. In the *Caelifera,* there is considerable variation in the basic form of the receptaculum seminis, and, although paired receptacula are not found, bifid or compound types are frequent in the two largest superfamilies *(Tetrigoidea* and *Acridoidea).* In other superfamilies, simple, single receptacula or anomalous forms occur.

So far as we are aware, the receptaculum seminis of *Tridactyloidea* has not hitherto been described, but in *Tridactylus thoracicus* Guérin-Méneville *(Tridactylidae)* it is in the form of a simple, narrow, elongate, coiled duct, at the end of which is a small, slender, hook-like loop, no wider than the duct, which may represent the spermatheca proper. However, in *Rhipipteryx* sp., there is an indication that the long narrow duct is really a spermathecal appendage as in that species it appears to arise sublaterally from a small pear-shaped swelling (the true spermatheca?) of a rather short, wider spermathecal duct. The duct in both genera opens into the large, wide atrium of the genital chamber. Behind the receptaculum seminis in *Tridactylus* (but not, apparently, in *Rhipipteryx)* is a single, unpaired, elongate, convoluted, sac-like 'ovipositor gland' similar in form and situation to the structure found in various *Gryllacridoidea* and *Tettigonioidea,* and presumably homologous with it — see Ander (1939) for references. This structure is of considerably greater diameter than the receptaculum seminis and opens medially by way of a short, narrow duct on to the ninth sternum. No such structure is known in other *Caelifera,* but the small, closely paired posterior diverticula found in *Tetrigidae* (Slifer, 1943 b) may conceivably be homologous with it.

In *Tetrigoidea (Tetrigidae)* the receptaculum seminis is clearly bifid in *Batrachideinae,* such as *Batrachidea, Tetrigidea* and *Scaria,* the secondary receptaculum forming a long, slender diverticulum (Slifer, 1943 b). In all three genera, the diverticulum joins the spermathecal duct not far from its orifice. In *Batrachidea* it bears a small apical bulb similar to that found in many *Acridoidea.* In *Scaria,* the primary receptaculum is almost as narrow as the secondary one and is apparently without a proper spermatheca; the latter joins the former so close to its orifice that paired receptacula are virtually present. The 'principal seminal reservoir' or spermatheca in *Tetrigidae* may have a caecum; in *Batrachidae* it is tricornute. In *Tetriginae,* such as *Tetrix* (Fenard, 1896; Slifer, 1943 b; Voy, 1949), *Nomotettix* and *Paratettix* (Slifer, 1943 b), the genital chamber is greatly extended anteriorly to form a large bursa. Although not a true 'bursa copulatrix', it con-

ceivably represents a much modified and enlarged terminal part of the spermathecal duct, to which the spermatheca is connected by a thin tube. There is no secondary receptaculum in this group. The spermatheca is elongate and curved and bears a reversely directed caecum, so that it is tricornute in form. The part of the spermatheca beyond the caecum is presumably homologous with the 'apical pocket' found in many *Acridoidea* (see p. 209). Slifer (1943 b) is rather dubious whether the organs acting as receptacula seminis in *Tetrigoidea* are, in fact, homologous with those of *Acridoidea,* but there would seem to be no strong grounds for such doubts.

In *Eumastacoidea (sensu* Kevan, 1966 h), there are also two general types of receptaculum: simple and compound. In *Eumastacidae,* so far as is known, the structure is simple and unpaired, consisting of a narrow spermathecal duct, recurved at the apex and bearing either a simple, pear-shaped or subspherical spermatheca (Slifer, 1943 b; Dirsh, 1951), or, in *Morabinae,* a large, elongate, simple sac (Blackith and Blackith, 1966 a).

In *Proscopiidae* there is a more complex organ. In *Proscopia scabra* Klug, the upper part of the moderately wide spermathecal duct is much lobed and bears a number of small short, curved, finger-like diverticula, one of which could conceivably (but probably does not) represent a reduced secondary receptaculum. The spermatheca proper is a rather large, tansverse sac with a small subterminal diverticulum at one end. A different arrangement is found in *Cephalocoema,* the only genus for which information has hitherto been published (Slifer, 1943 b). This is perhaps best interpreted as representing two rather narrow receptacula (the primary one having a distinct, small spermatheca with a lateral caecum) leading into the side of an elongate, swollen atrium (representing the terminal part of the primary spermathecal ducts). The impression is thus given of three spermathecae of differing forms all leading into a very short, swollen, common duct, but the largest of the three may be regarded as a 'bursa' analogous to that mentioned above for *Tetriginae.*

The *Tanaoceroidea (Tanaoceridae)* have a very simple, single, receptaculum seminis, consisting only of a thin spermathecal duct into which, at right-angles, opens an ovoid vessel termed the "diverticulum" by Rehn and Grant (1960 b). Whether this represents the spermathecal vesicle proper or the caecum of the spermatheca of *Acridoidea* (see below) is a moot point.

The *Pneumoroidea* [*sensu* Uvarov (1966) not Dirsh (1966 b)] *(Pneumoridae)* have two types of receptaculum (Dirsh, 1957, 1965 a). The spermatheca may be long and slender or short and stout, but, in either case, it is beset with diverticula (narrow and wide apart in the former; lobe-like in close together in the latter instance). It could conceivably be that one of the lower diverticula represents the secondary receptaculum and that the remainder are branches of the primary spermatheca and/or its caecum, the latter having taken up an apical position as in many *Acridoidea*. This is, however, entirely speculative.

In *Acridoidea, s. str.*, the receptaculum seminis is very variable in form. In some families there may be no direct evidence for a compound structure; in others, such evidence is uncommon or inconclusive; but in most *Acrididae* there is a bifid spermatheca. *Pyrgomorphidae* show almost every degree of variation from the simplest form without a diverticulum (or even a caecum) in which the spermatheca is so reduced as to be virtually a mere continuation of the duct, by way of simply curved C- or S-shaped spermathecae, to bifid forms with or without secondary diverticula. A secondary receptaculum, if present, may be closely associated with the principal seminal reservoir, but rarely (some *Nereniini)* it may be quite separate, forming a lateral diverticulum of the lower part of the main spermathecal duct, rather similar to the condition noted for the *Ensifera* in *Tachycines* (see p. 199).

Acridoidea, s. str. Packard (1878) seems to be the first to have paid much attention to the receptaculum seminis of the *Acridoidea*. In a drawing by E. Burgess (who rarely, if ever, seems to be given due credit) he published a small, but essentially accutate, figure of *Melanoplus femurrubrum* (DeGeer) *(Acrididae)*. However, he misinterpreted the function of the spermatheca, designating it as a sebific (or sebaceous, or colleterial) gland; the dilation on the spermathecal ("sebific") duct, just above its orifice, he incorrectly called a "bursa copulatrix". Berlese (1882) refers to 'la spermateca' in several genera of *Acrididae,* namely, *Anacridium* [as *Acrydium*], *Calliptamus* [as *Caloptenus*], *Locusta* [as *Oedipoda*], *Gomphocerus* [?], and *Truxalis,* but he is usually imprecise regarding which genus formed the basis of any particular observation. In the case of the first two genera, however, he notes that the terminal part of the spermathecal duct is enlarged and hardened. Peytoureau (1895) also calls this region the "zone indurée" in *Dociostaurus* [as *Stauroderus*] *maroccanus.* Fenard (1896) studied the receptaculum seminis of a number of *Acrididae* in

some detail and introduced an elaborate terminology for the various parts. He noted that, in *Acridium* [= *Anacridium*] *aegyptium* and *A. peregrinum* Olivier [= *Schistocerca gregaria*], the spermathecal duct has a large dilation just above the orifice, but that *Caloptenus* [= *Calliptamus*] *italicus* (Linnaeus) has only a small swelling in this region. These three species are said to lack an "éperon" ('spermathecal appendage' of the present work — see p. 208), but Fedorov (1927) and Slifer (1939) indicate this to be incorrect. Sokolow (1926) and Boldyrev (1929) also discuss the receptaculum in *Locusta,* although not very precisely.

It would serve no useful purpose to review all the literature referring to the receptaculum seminis in *Acridoidea,* but several morphological works are of significance. That of Nel (1929), who gives the first detailed account of the development of the organ, with particular reference to *Locustana pardalina (Acrididae),* is of interest here because it is also the first work to mention a member of the *Pyrgomorphidae (Colemania sphenarioides)* in this connection. For *Acrididae,* Snodgrass (1935 b) discusses the receptaculum in *Dissosteira* and *Melanoplus;* Guarino (1935) includes a description of the structure in his account of the female genitalia of *Anacridium aegyptium;* Paoli (1937) and Jannone (1939) refer to its anatomy and histology in *Dociostaurus maroccanus;* and Voy (1949) describes it for several acridid genera. More recent anatomical studies of individual species of *Acrididae* that refer briefly to the receptaculum seminis are those by Albrecht (1953), Mika (1959), Thomas (1963) and Gregory (1965), all for *Locusta migratoria,* by Albrecht (1956), for *Nomadacris septemfasciata* (Audinet-Serville), and by Thomas (1965), for *Schistocerca gregaria.* Gregory's account is the most detailed and introduces a number of new (English) terms for different parts, particularly of the spermathecal duct.

The possible taxonomic significance of the concealed female organs of *Acridoidea* was indicated first by Vardé (1934) following an earlier work by the same author (Vardé, 1929). Slifer and King (1936) then made a preliminary survey of the various groups, which, like the work of Vardé (1934), was concerned almost entirely with the presence or absence of the glandular pouches now known as Comstock-Kellogg glands (see p. 191). This survey resulted in a series of well illustrated papers by Slifer (1939, 1940 a, b, 1943 a, b) which also dealt extensively with the receptaculum seminis, the last paper in the series dealing only with *Caelifera* other than *Acridoidea* as presently understood.

These investigations suggested a classification of the *Acridoidea* based primarily on the presence or absence of Comstock-Kellogg glands and indicated that the spermatheca might provide additional taxonomic characters. Roberts (1941), however, was of the opinion that the form of the spermatheca, rather than the presence of glandular pouches, should be considered as being of primary importance. Voy (1949), who studied the entire female genitalia in the main groups of orthopteroid, insects, concluded that the form of the receptaculum seminis is very characteristic for each 'suborder' and even 'family' (the terms referring approximately to pesent orders and superfamilies), but only a few species were investigated, so that no valid conclusion could be drawn regarding the importance of the structures within the *Acridoidea.*

Although the spermatheca and associated structures of various *Acridoidea* had been described earlier, as noted above, it was not until recently that their use in taxonomy became at all general. Kevan (1952 a) indicated that the spermatheca of *Xyronotus* (now *Xyronotidae)* was, as had been shown by Slifer (1943 a), simple and quite comparable with those of certain *Pyrgomorphidae* and some *Pamphagidae.* He further indicated that *Trigonopterygidae* have a simple spermatheca, which may be greatly dilated [it is not always so, see Kevan (1966)]. The same author (Kevan, 1952 b, 1953, 1959) also showed that members of the pyrgomorphid tribe *Chrotogonini (Chrotogonus,* with its subgenus *Obbiacris, Tenuitarsus* and *Stibarosterna)* all have similar spermathecae. Márquez Mayaudón (1967) used the spermatheca among other characters, to distinguish between species of the pyrgomorphid genus *Sphenarium.*

Katiyar (1936) described and figured the spermathecae of various Indian *Acrididae* and confirmed that, as was previously indicated by Slifer (1939, 1940 c) and subsequently by Kevan (1966 g), there may be appreciable variation within species, so that the precise form of the spermatheca would seem to have limited taxonomic usefulness at the species level. Dirsh (1957), however, indicates that the spermatheca provides useful taxonomic characters at higher levels, although caution is required in using it because of the lack of uniformity within certain families, notably *Lentulidae, Pyrgomorphidae* and romaleine *Acrididae.* Barnum (1959) dismisses the character as valueless at the species level in oedipodine *Acrididae,* but Rehn and Grant (1959 a-c, 1960 a, c) make use of it in *Romaleinae* and *Gomphocerinae (Acrididae).* Dirsh

(1961, 1963 a-c, 1964 a, 1965 a-c) also found it advantageous to figure the spermathecae form many genera of *Acridoidea* belonging to several families, and for *Pneumoroidea*. Banerjee and Kevan (1962) note that the spermatheca of the pyrgomorphid *Atractomorpha lata* (Motschoulsky) is similar to that of *A. ambigua* Bolívar (= *A. sinensis* Bolívar); Eades (1902) discusses briefly similarities in the *Dericorythinae (Acrididae)*, figuring the structure in *Conophyma semenovi* Zubovskiĭ; Rehn and Randell (1963) figure it for several species of *Melanoplini (Acrididae)*; Kevan (1966 c) illustrates the spermatheca and ducts for three genera and four species of *Trigonopterygidae;* and Kevan (1966 a , b, e-g) has made extensive use of the spermatheca in his studies of various genera of *Pyrgomorphidae*. Descamps and Wintrebert (1966 b) illustrate the receptaculum seminis for several members of this family and of the *Acrididae*.

Uvarov (1966) has summarized the taxonomic position by stating that "the distal part of the spermathecal duct" (i. e. the spermatheca as here understood) is subject to considerable variations among various *Acridoidea* and that these variations are characteristic for some groups [both higher and lower].

d) *The Spermathecal Duct.*

The duct connecting the spermatheca with the genital chamber is divisible into several regions. In *Truxalis nasuta* (Linnaeus), Fenard (1896) recognized three parts: a wider region nearest the orifice ("renflement sus-oviductal"); anterior to this, a narrower tube — with a lower, twisted part ("spirale") and an upper, straighter region ("canal séminal filiforme") —; and finally, below the "réservoir séminal", a region comprising several coils ("tortillon"). For *Dociostaurus maroccanus,* Paoli (1937) also refers to three parts of the duct; "tubo crasso", "tubo tenue", and "tubo collegato", corresponding approximately to Fenard's three regions. Voy (1949), for *Stenobothrus lineatus* (Panzer), uses much the same terminology as Fenard *(l. c.)*, but he omits special reference to the first section and refers to the "canal" without qualifying words; he also substitutes "spire terminale" for "spirale". Mika (1959) and Gregory (1965), in their studies on *Locusta* used German and English terms for regions approximately corresponding to the French and Italian respectively. Gregory *(l. c.)*,

however, introduced several other special terms: "triangular sclerotized plate", "vestibule" and "first bend". The last constitutes part of Fenard's "spirale".

The first of Gregory's special terms just noted is included under 'spermathecal valve' in the present work, as the term used for *Locusta* is not generally applicable. Gregory's "first bend" is here called the 'final bend' because it is the last (not the first) if it is considered from the viewpoint of female anatomy and physiology, rather than of the intromission of the spermatophore by the male. It is for the same reason that ambiguous words 'distal' and 'proximal' are here avoided. 'Proximal' in particular, has been used by previous authors (e. g. Slifer, 1939, 1940 a, b, 1943 d) to indicate the intromittal end of the duct, which is, in fact, the most posterior and anatomically the most distal. The terminology adopted here is illustrated in Fig. 2, *B* and, with the exceptions noted, is generally based upon that of Gregory *(l. c.)*. The terminology used by other authors is included under the currently accepted terms defined on pp. 240-248.

In most *Pyrgomorphidae* the various parts of the spermathecal duct are generally identifiable, although some of them are not always very clearly differentiated. For the most part, they are not discussed further in this work. The 'thick tube' ('tubo crasso') or terminal part of the spermathecal duct (Fig. 2, *B,* TP), however, will be referred to occasionally. In the vicinity of the orifice (O), also, there is often a conspicuous 'terminal dilation of the spermathecal duct' (TD), which will be mentioned for several genera; the spermathecal valve (SV) is occasionally well developed, and will likewise sometimes be referred to. An appendage of the spermathecal duct is found in a few genera of *Nereniini,* but, as previously noted, this represents the secondary receptaculum seminis in its most primitive position in *Acridoidea,* and, as it is homologous with what is here termed the 'spermathecal appendage' (SA), discussion of it is deferred until the next section.

e) *The Spermatheca.*

General structure and variation. As already noted (p. 197), there has been imprecision in the literature regarding how much of the receptaculum seminis is indicated when the term 'spermatheca' (or its vernacular equivalent) is used. In the present work, therefore, the

term includes only the 'body' or 'head' of the receptaculum and not its duct. If associated structures ('appendage', 'caecum', 'diverticula') are also to be excluded, the term 'spermathecal vesicle' is used. In some instances it is difficult to determine just where the vesicle ends or the associated structures begin, and, if there has been an anatomical shift, to be certain of homologies, but, in general, difficulties of this kind can be resolved, at least arbitrarily.

Two main regions of the spermatheca, as here restricted, were first distinguished for *Acrididae* of Fenard (1896) as "réservoir séminal (proprement dit)" — a comparatively large, subterminal, lateral vessel — and "éperon" — a narrow 'spur' running in roughly the same direction as the spermathecal duct and apparently continuous with it. These two parts have received other names in the past (see glossary pp. 240-248), but those that have been most generally employed by authors writing in English, have been "preapical diverticulum" and "apical diverticulum" respectively. These were introduced by Slifer (1939) and used by her and other authors subsequently. However, in the present work, Slifer's terms have been discarded for the reasons noted below.

When the *Acridoidea* are considered as a whole, homologous structures may take up different positions so that such epithets as 'preapical' and 'apical' are often inappropriate. The "apical diverticulum" is in any case basically lateral, or conceivably dorsal, but not apical, in origin, its apparent apical position being more or less confined to *Acrididae,* and then chiefly when it is relatively small. The "preapical diverticulum", particularly in the absence of the "apical" one, may be continuous with the rest of the receptaculum seminis and hence, itself, 'apical'. Dirsh (1957) thoroughly confused the two terms, except possibly in a topological sense. Even the term 'diverticulum' is scarcely appropriate in either case, even if it is often convenient, because the so-called "apical diverticulum" is apparently homologous with the second (or secondary) receptaculum seminis (whatever its origin) and not (we believe) an outgrowth of the primary one. Similarly the so-called "preapical diverticulum" is apparently most often a composite structure (see below), not entirely an accessory outgrowth. For this latter structure, therefore, we prefer to revert to a version of Fenard's (1896) term, qualified as by Voy (1949), and to call it the "principal seminal reservoir". Unfortunately, Fenard's original terms "éperon", or in English, "spur", is inappropriate for the "apical diverticulum",

because, although it avoids positional implications, it suggests a short, simple structure which the organ in question may frequently not have. 'Spermathecal appendage' is therefore used here — earlier alternatives implying a glandular nature for the structure, such as 'spermathecal gland' (see glossary, p. 246), are avoided because any gland (i. e. glandular tissue) that may be associated with the organ is not included in the chitinous parts to which we refer here. Further, the term 'spermathecal gland' (of Nel, 1929) would infer functions and homologies that are not established.

In many *Acridoidea,* the spermathecal appendage is absent, but, in others, there may be a small apical pouch or swelling which suggests that it might represent an 'incipient', or reduced, spermathecal appendage. In *Acrididae* of the closely related subfamilies *Oedipodinae, Gomphocerinae* and *Egnatiinae,* this is undoubtedly the case, but, in other groups, the pouch almost certainly represents the true apex of the receptaculum seminis and is here termed the 'apical pocket of the spermatheca'. That it is not a reduced appendage as indicated by the fact that a true spermathecal appendage may also be present. Even a few species belonging to the subfamilies mentioned above that have a greatly reduced spermathecal appendage, may also have an apical pocket, although this is unusual. In the absence of an apical pocket, the principal seminal reservoir may often appear to form a single, undifferentiated, curved vessel, but, where the pocket is present, two regions may be defined; the true spermatheca, or, as here termed, the 'spermathecal vesicle', lying immediately above the spermathecal duct (and 'vestibule') and including the apical pocket; and a subapical appendicular part, or 'caecum of the spermatheca' (equivalent to most of the "preapical diverticulum" of other authors). Secondary diverticula may be present on both the spermathecal appendage and the principal seminal reservoir. These vary considerably in form and position, and sometimes their homologies are difficult to determine. The terminology here used is illustrated in fig. 2 *B*.

In order to understand the homologies of the different parts of the varied pyrgomorphid spermathecae, it is now appropriate to discuss the acridoid spermatheca in general. Fig. 2, *B,* shows a schematic receptaculum seminis from which virtually all types may be derived and which incorporates the main features found in *Pyrgomorphidae* as well as in other families. Practically all forms of receptaculum seminis known in *Acridoidea* (and possibly in most other orthopteroid insects)

can be shown to have a homologous structure, their parts differing only in position and degree of development or of suppression (usually the latter). Whether the ancestral acridoid had indeed anything approaching the form of spermatheca shown (particularly the secondary diverticula which have been added for completeness) is questionable, but the diagram at least provides a base-line from which discussion can proceed. It may also be observed that the diagram is not altogether hypothetical because spermathecae of rather closely comparable forms are found in several different subfamilies of *Acrididae,* e. g. in *Dericorythinae (Iranella eremiaphila* Uvarov) — see Slifer (1939: pl. 5, fig. 82; Eades, 1962), in *Hemiacridinae (Paulianacris hirsuta* Dirsh) — see Descamps and Wintrebert (1966 b), in *Coptacrinae (Coptacra foedata* [Audinet-Serville]) — see Slifer (1940: pl. 4, fig. 38), in *Eyprepocnemidinae (Tylotropidius* sp.) — see Slifer (1940 b: pl. 8, fig. 119), in *Catantopinae (Netrosoma fusiforme* Scudder) — see Slifer (1943 a: pl. 1, fig. 9), and even in *Romaleinae (Diponthus)* — see Rehn and Grant (1959 a) — although this genus is probably not a romaleine (see p. 216) — as well as in *Pyrgomorphidae* such as *Atractomorpha.* Only the last example may have so long a spermathecal appendage, or secondary diverticula, but these are found in numerous unrelated genera of *Acridoidea* whose spermathecae are otherwise somewhat less 'diagrammatic'.

In the schematic representation of the receptaculum seminis (Fig. 2, *B),* what may be termed the 'head of the receptaculum', or spermatheca in the wide sense, consists of the three parts already discussed above: the spermathecal vesicle (SP); the caecum of the spermatheca (SC); and the spermathecal appendage (SA). As already noted, it may sometimes be difficult to determine where the spermathecal vesicle ends and the caecum begins, but this is easily done where the true apex of the spermatheca is indicated by the presence of an apical pocket (APO), which, unfortunately, is not always the case. Below the spermathecal vesicle is a short, usually somewhat dilated region of the spermathecal (SD), the vestibule (VE), and it is frequently just above this region that the spermathecal appendage (SA) is attached. There may, however, be considerable migration of the latter upwards even to the extent of passing around the apex of the spermathecal vesicle (as has been discussed for *Ensifera,* pp. 199-200), and occasionally on to the

caecum. The reverse may also occur (see p. 214). The appendage very often has at its apex a small subspherical swelling, the apical bulb (AB), homologous with the secondary reservoir in other orthopteroids (Voy, 1949). When present (many *Acrididae* and *Pyrgomorphidae),* this can be a useful marked enabling one to determine which part of the entire organ is, in fact, the appendage and thus homologous with the secondary receptaculum. The secondary diverticula (SB and SL) on the caecum and spermathecal appendage (more rarely on the spermathecal vesicle or vestibule) are probably not basic structures, but they are sufficiently widespread and common to be included in a diagramatic representation.

It will be appreciated that all the features shown in Fig. 2, *B,* are not distinguishable in all genera, or even in all groups. Thus, as already noted, the spermathecal appendage may frequently be absent or greatly reduced (see p. 209). Not infrequently both it and the apical pocket are suppressed, but it is rare for there to be no structure homologous with the spermathecal caecum, even although it is commonly undifferentiated from the apex of the spermathecal vesicle. Only where the spermatheca is not recurved in any way, as in *Psednura* and *Modernacris* (both *Pyrgomorphidae),* would it seem to be truly absent in *Acridoidea.* In the former genus the whole spermatheca is represented only by a minute swelling; in the latter, it is enormous and forms an erect bladder-like structure, presumably representing only the spermathecal vesicle. *Modernacris* and some other *Nereniini* are also unusual in that the spermathecal appendage is not associated with the head of the receptaculum, but maintains its primitive position well down the spermathecal duct (cf. *Tachycines,* p. 199).

Throughout the *Acridoidea* there is great variation in the form of the spermatheca (Slifer, 1939, 1940 a, b, 1943 a; Dirsh, 1957), the greatest diversity being found in the *Pyrgomorphidae* and *Lentulidae.* All parts of the spermatheca are subject to this variation, which may take the form of reduction or atrophy (as already noted), amalgamation of adjacent parts (as in the case of the vesicle and its caecum), or by hypertrophy. This last usually takes the form of increase in length and may affect particularly the spermathecal appendage or the caecum (as well as the spermathecal duct). The caecum may sometimes become hypertrophied by inflation (exaggeratedly so in *Trigonopteryx hopei* Westwood *(Trigonopterygidae))* — see Kevan (1952 a, 1956 c). The spermathecal vesicle rarely hypertrophies, but

it may do so in *Nereniini* (see above). The apical pocket of the spermatheca, as a distinct entity, is rarely enlarged, and then only to a small degree by elongation, e. g. in *Aeroloplus* and *Caudellacris (Acrididae)* — see Slifer (1940 b; pl. 3, fig. 21; pl. 4, fig. 34); it may occasionally become latterally displaced as in *Apallachia arcana* Hubbell and Cantrall *(Acrididae)* — see Slifer (1940 b; pl. 2, fig. 24). The apical bulb of the spermathecal appendage quite frequently disappears, particularly, but not only (or always), when the diverticulum is short or very slender; occasionally however it is relatively quite large, as in the last species referred to. Secondary diverticula in the form of lobes or less commonly, branches, varying from mere bulges to long vermicular structures, are found sporadically throughout several families (Slifer, 1939, 1940 a-c, 1943; Dirsh, 1957; Rehn and Grant, 1959 b). The highest degree of complexity is met in *Dictyophorus (Pyrgomorphidae)* in which lobes and stout branches, often with subsidiary lobes, arise from all parts of the spermatheca (Slifer, 1940 a; pl. 3, fig. 23 [as *Tapesia*]). In *Teratodes* and *Acrostegastes (Acrididae, Teratodinae)*, there is also a complex system of branches, but in this case, it is confined to the spermathecal appendage (Slifer, 1940 b; pl. 8, fig. 112; Rehn and Grant, 1959 b).

Variation in different groups of Acridoidea. The spermathecae of *Caelifera* other than *Acridoidea* have already been shown to differ widely between and within groups, and the same is true within the *Acridoidea.* The following is a brief review of the characteristic forms of spermathecae found in different families. The sequence in which the families are treated here has no special significance; it is merely convenient. The *Lentulidae* and *Pyrgomorphidae* which show the greatest diversity are left until last.

The *Xyronotidae,* an anomalous family with one genus only, have a simple S-shaped spermatheca (Slifer, 1943 a, Kevan, 1952 a), the end of which represents an undifferentiated spermathecal caecum. Similar spermathecae are found in other *Acridoidea,* particularly in *Pyrgomorphidae.* There is no trace of a spermathecal appendage. The *Trigonopterygidae* are basically similar (Kevan, 1952 a, 1966 c; Dirsh, 1957, 1961), although the size of the part that may be called the caecum varies very greatly and may be much inflated.

Pamphagodidae (syn. *Charilaidae)* have a prominent apical pocket and a distinct, C-shaped caecum (Dirsh, 1957; Descamps, 1966). In *Pamphagidae* — with which Eades (1963) reunited the last family (see

also Descamps, *l. c.)* — an apical pocket is seldom distinct or even present, although it is prominent in *Thrinchus* (Slifer, 1940 a); the caecum varies from a simple U- or S-shaped body to a long, thick, twisted sac, sometimes bearing a number of pocket-like secondary diverticula on the outer curve. *Lathiceridae* have a simple S-shaped spermatheca in which the caecum is marked off from the spermathecal vesicle by an indication of an apical pocket (Dirsh, 1957). None of these families has any trace of a spermathecal appendage.

The receptacula seminis of typical *Ommexechidae* are very characteristic and highly peculiar (Slifer, 1940 b). Most of the spermathecal duct is probably homologous with the 'thick tube' (Fig. 2, *B*, TP) and is considerably dilated and doubled back upon itself (in *Ommexecha* the two arms of the loop thus formed are fused to form a single, large 'bursa'). The remaining part of the duct ('thin tube' and 'constricted tube', TT, CT) is quite short and the head of the spermatheca relatively small. The latter comprises the spermathecal vesicle (with a finger-like apical pocket), a C- or S-shaped caecum (with a small secondary diverticulum in *Spathlium)*, and a narrow, finger-like spermathecal appendage (absent in *Parossa* [= *Clarazella*]*)*. The impression is given of small claws set on a thin stalk; Slifer *(l. c.)* sees a fanciful resemblance to a "human hand" (with only two or three fingers?)! Eades (1961 a) added certain anomalous genera to the *Ommexechidae,* including *Conometopus* and *Aucacris,* both of which have typically acridid spermathecae. That of the latter genus is not figured by Eades *(l. c.),* but by Dirsh (1964 c), who indicates that *Aucacris* is not an ommexechid. If the spermatheca is any guide, neither is *Conometopus.* The other small, peculiarly South American family, the *Pauliniidae,* has spermathecae which do not differ from some of the more reduced types found in *Acrididae* (notably *Oedipodinae)* — see Slifer (1939). It is not unlikely that members of this family are but specialized *Acrididae* and that they do not deserve separate family status (Eades, 1961 a).

With the exception of most *Romaleinae* and *Teratodinae* (see below), the *Acrididae* almost all have spermathecae conforming to a common pattern, incorporating the spermathecal vesicle (most often not well defined, but sometimes clearly indicated by the presence of a distinct apical pocket), a simple, usually sac-like caecum, and a spermathecal appendage of variable length and diameter. In *Netrosoma fusiforme (Catantopinae* — see p. 210) an almost schematic arrangement is found, except that the spermathecal appendage is rather short and

lacks a distinct apical bulb. It is, however, rather unusual among *Acrididae* (other than some *Romaleinae*) in that the caecum is doubly curved. *Iranella eremiaphila (Dericorythinae* — see p. 210) is very similar, except that the spermathecal appendage is even shorter and the end of the caecum recurved in the reverse direction from that of *Netrosoma;* in *Conophyma* (another member of the *Dericorythinae*), the spermathecal appendage is quite long, although the caecum is much less sinuous (Eades, 1963).

Xiphophora cyanoptera Gerstaecker *(Catantopinae)* — see Slifer (1943: pl. 2, fig. 19) — and *Chrysochraon dispar* (Germar) *(Gomphocerinae)* — see Voy (1949) — have serpentine caeca, but only short spermathecal appendages; there is no apical pocket. *Paulianacris hirsuta* Dirsh *(Hemiacridinae)* and *Pseudohysiella inermis* Dirsh *(Catantopinae)* are somewhat similar, but, especially in the latter have longer *appendages* (without an apical bulb) — see Descamps and Wintrebert (1966 b). *Appalachia arcana* (see p. 212) and *Boonacris glacialis canadensis* (Walker) *(Cantantopinae)* — see Slifer (1943 a: pl. 2, fig. 20 [as *Zubovskya*]) — have normal caeca, but somewhat exaggerated apical pockets and long spermathecal appendages with enlarged apical bulbs. One species assigned to *"Opshomala" (Catantopinae)* [but presumably not a member of that genus — see Rehn and Eades (1961 a)] has a very elongate caecum and a very narrow, minute spermathecal appendage (Slifer, 1943 a: pl. 1, fig. 12), and *Sedulia specularia* Stål *(Catantopinae)* — see Slifer (1940 b: pl. 8, fig. 110) — has an unusually large vestibule. In some species of *Melanoplus (Catantopinae)* it would seem that the caecum of the spermatheca has migrated around the apex of the spermathecal vesicle to become associated with the lower part of the spermathecal appendage (Slifer, 1940 b: pl. 6) — the reciprocal of the displacement that has occurred in some *Pyrgomorphidae* (see p. 218). The spermatheca of *Acrophymus (Euryphyminae)* is described by Dirsh (1963 c) as having a "two-branched diverticulum and an additional third branch", but it in fact conforms closely to the basic plan: a prominent appendage with a marked apical bulb; a distinct spermathecal vesicle with an obvious apical pocket; and a subapical, recurved caecum. Secondary diverticula are found in a few genera, e. g. *Pardalophora haldemanni* (Scudder) *(Oedipodinae)* and *Urnisa guttulosa* Walker *(Catantopinae)* — Slifer (1939: pl. 5, fig. 89, 90; pl. 6, fig. 100) — and in *Hieroglyphus concolor* Walker *(Hemiacridinae)* — see Katiyar (1956). In the first two species, these are asso-

ciated with the vestibule and upper part of the spermathecal duct; in the last, with the upper part of the spermathecal appendage.

By and large, there is less diversity in *Acridinae, Oedipodinae, Truxalinae, Gomphocerinae* and *Egnatiinae* (all of which are rather closely related) than in any but the smallest of the other subfamilies of *Acrididae,* and there is a greater tendency for the spermathecal appendage to become greatly reduced, as in *Stethophyma lineatum* (Scudder) and *Oedipoda miniata* (Pallas) *(Oedipodinae)* — see Slifer (1939: pl. 3, fig. 56; pl. 5. fig. 86). This modification may also occur in *Catantopinae,* but rather infrequently, for example in *Vilerna* (Slifer, 1940 a: pl. 8, fig. 120; 1943 a: pl. 2, fig. 18), in which the spermathecal appendage may be completely lost. Dirsh (1957, 1961) indicates that *Lithidium* (now removed from the *Lentulidae* to the *Acrididae-Lithidiinae)* also lacks a spermathecal appendage, although *Eneremius,* tentatively placed with it, has one (Dirsh, 1957). In the small subfamily *Egnatiinae,* the spermathecal appendage is also completely lost in *Egnatioides farsistanicus* Uvarov and *Charora pentagrammica* Bolívar (Slifer, 1939: pl. 4, figs. 70, 73) although in *Egnatius* it is present, though small. *Chilacris (Tristirinae* — syn. *Chilacridinae)* is another genus which lacks a spermathecal appendage (Dirsh, 1961).

The *Romaleinae* and the *Teratodinae* — included in the same subfamily by Dirsh (1956. 1957, 1961, 1965 b), Uvarov and Dirsh (1961) and Uvarov (1966), but not by Rehn and Grant (1959 b) — have spermathecae that, in all but a few genera, are quite different from those of most other *Acrididae.* In the latter subfamily, there is always a long, convoluted spermathecal appendage, which, except in *Lyrostyloides,* is branched. This is particularly the case in *Acrostogastes* (Rehn and Grant, *l. c.)* and *Teratodes monticollis* (Gray) (Slifer, 1940: pl. 8, fig. 112; Rehn and Grant, *l. c.);* there is but one short secondary diverticulum in *Kabulia* (Sliger, 1940 b: pl. 5, fig. 61). It may, however, be noted that short, secondary diverticula on the spermathecal appendage are not peculiar to *Teratodinae,* as they are also found in a few other unrelated genera of *Acrididae,* e. g., in *Melanoplus (Catantopinae)* and *Hieroglyphus (Hemiacridinae)* — see Slifer (1940 c) and Katiyar (1956) — although they, and the spermathecal appendage, differ in form. In all *Teratodinae* also, the spermathecal caecum is U-shaped and the apical pocket suppressed.

In the largely, if not wholly, American subfamily *Romaleinae,* the spermatheca is usually more or less reminiscent of what is found in

Pamphagidae, except that an apical pocket is usually distinct and there are no diverticular pockets on the caecum (Slifer, 1940 a, 1943 a; Rehn and Grant, 1959 a, c, 1960 a; Kevan, 1967); several genera of *Pyrgomorphidae* have very similar spermathecae. The romaleine genus *Colpolopha* includes at least one unusual species, *C. obsoleta* (Audinet-Serville) in which there is a long, slender spermathecal appendage *(C. bruneri* Rehn is more typical and has none) — see Rehn and Grant (1959 a). *Diponthus* (see p. 210) has a G-shaped caecum and a short spermathecal appendage with an apical bulb, but apparently no distinct spermathecal vesicle or apical pocket. The genus, however, also has anomalous phallic structures (Rehn and Grant, *l. c.)* which caused Dirsh (1956) to place it in the *Catantopinae, sens. lat.* Its spermatheca also is certainly more catantopine than romaleine. We agree with Uvarov and Dirsh (1961) that this genus should not be retained in the *Romaleinae. Antandrus* (= *Batrachacris)* also has an unusual spermatheca for the *Romaleinae* as there is a short, thick spermathecal appendage (conceivably, however, this may be an elongated apical pocket) and a rather short, only slightly curved caecum (Slifer, 1943 a; pl. 1, fig. 1; Rehn & Grant, *l. c.).*

Unlike those of the groups already mentioned, the spermathecae of *Lentulidae* and *Pyrgomorphidae* do not exhibit characteristic general patterns throughout each family. In the former the form of the spermatheca is less varied, perhaps only because of the small size of the group, and there are certainly some very peculiar departures from the conventional. There are two groups of *Lentulidae:* those with spermathecal appendages and those without (Dirsh, 1955). In *Lentula, Rehnula* and *Eremidium,* the spermatheca is of a single S-shape, similar to that found in several other families, without an apical pocket and varying only in proportions; in *Sygrus rehni* Dirsh, the form is similar, but Dirsh *(l. c.)* shows the thin tube of the spermathecal duct issuing laterally from the end of the thick tube; in *Paralentula* there is a slight indication of an apical pocket and the spermathecal caecum is rather irregularly coiled; in *Gymnidium* there is no apical pocket and the caecum is saussage-shaped; in *Betiscoides* it is similar with a pointed apex. All these genera lack a spermathecal appendage. In *Devylderia* (Dirsh, *l. c.)* and one species of *Mecostibus* (Slifer, 1940 b: pl. 5, fig. 64), there is a fairly conventional arrangement incorporating a long, coiled spermathecal appendage and a large, rather straight, caecum arising from the spermathecal vesicle. In *M. minor* (Bruner),

however, Dirsh's *(l. c.)* figure is more difficult to interpret; there would appear to be a similar arangement to the above (although the parts of the spermatheca are reduced in size), but a second, larger appendage is also shown arising well down the spermathecal duct. If the drawing is correct, we have here two widely separated spermathecal appendages, the like of which is not known to us elsewhere in the *Orthoptera,* unless it be in a modified form in one or other of the two following species. Clearly one or other appendage must be a secondary development. The spermathecae of *Basutacris scotti* Dirsh and *Swaziacris burtti* Dirsh may be interpreted in different ways. In both there are three branches, of which the lowest could be considered to be a secondary appendage, such as discussed above for *Mecostibus minor,* but forming part of the head receptaculum seminis. This would permit one to interpret the other two branches as the (primary) spermathecal appendage and the spermathecal caecum. However, we believe that, in *Basutacris,* the lowest branch, which is very short and slender, is the spermathecal appendage, that the next, somewhat larger, curved branch represents the spermathecal vesicle, from which the third and largest, rather straight branch arises near its base as the spermathecal caecum. It could, however, be that the second branch is a secondary diverticulum of the caecum or of the spermathecal vesicle, or even that the largest branch is the spermathecal vesicle and that this bears a smaller, curved caecum. In *Swaziacris,* although there are also three branches, they are all vermiform and very similar (although Dirsh shows one as being straight and the others coiled). Again there are the several possible interpretations with the additional possibility that there is a simple, coiled spermatheca without a caecum, but with a branched appendage! Only a re-examination of these and other lentulid spermathecae can help to resolve these problems of homology.

In the *Pyrgomorphidae,* the majority of genera have a simple sometimes rather irregular, S-, C-, or G-shaped spermatheca without a spermathecal appendage, but very often with an apical pocket clearly demarcating the caecum from the spermathecal vesicle (Slifer, 1940 a: pl. 3, figs. 18-22, 24, 25; Dirsh, 1963 b). In some the pocket may be very prominent (e. g. *Tagastini, Poekilocerini, Phymateini);* in others, although the apical pocket is not specially pronounced, the spermathecal vesicle is noticeably wider than the base of the caecum *(Omurini).* Mitricephalini have a very short, undifferentiated caecum; *Acanthopyrgus (Sagittacridini)* and *Sphenarium (Sphenariini)* have a rather

inflated one; and, in *Chrotogonini,* the caecum has a curved, finger-like apical process (which may represent the last vestige of a greatly displaced spermathecal appendage — see below). Very simplified types of spermatheca include those of *Megra* and *Nerenia (Nereniini), Psednura* and *Propsednura (Psednurini),* in which the whole structure is reduced to a small bulb. In the first two genera, the whole receptaculum (including the spermathecal duct) is inordinately long (Kevan, 1966 b) and may not be as simple as it would appear (see below); in *Psednura* the duct is very short. In *Verduliini* (Kevan, 1966 b), the caecum of the spermatheca varies from a moderate-sized, irregularly shaped sac to a small finger-like process at the apex of the spermathecal vesicle. In *Apodesmoptera,* it is in the form of a large, elongated apically inflated sac (Kevan, 1966 h), quite different from what is found in other *Desmopterini* (Kevan, 1966 a), although conceivably of similar origin.

A large number of *Pyrgomorphidae* do not have such simple spermathecas as those already referred to, but possess spermathecal appendages or what are believed to be homologous structures. In *Modernacris* the spermathecal duct is comparatively short and bears a vermicular, spermathecal appendage considerably removed from the spermatheca, and the spermathecal vesicle is enormously inflated, lacking a caecum (Dirsh, 1964 a; Kevan, 1966 g; and p. 211); *Oxytarbaleus* seems to be similar; *Buergersius* also has a vermiform lateral appendage arising from the spermathecal duct, but the nature of its spermatheca is uncertain (Kevan, *l. c.*). *Noonacris,* has a shorter, wider spermathecal appendage nearer to, but still remote from, the spermathecal vesicle, which is much less inflated, but which bears laterally at its apex a large, simple, swollen caecum. These four genera all belong to the *Nereniini,* but other members of that tribe have quite different spermathecae (see below).

The only other genera of *Pyrgomorphidae* that have an unmistakable spermathecal appendage are *Atractomorpha (Atractomorphini)* (Slifer, 1943 a; Banerjee and Kevan, 1962; Dirsh, 1963 b) and *Occidentosphena* (currently tribe *Occidentosphenini,* but probably better regarded as a subtribe of *Atractomorphini).* In these, the arrangement conforms closely with the schematic model (Fig. 2, *B*), even to the extent that secondary diverticula may sometimes be present. A distinct apical pocket of the spermathecal vesicle and a small apical bulb on the spermathecal appendage are also found in one or two species of *Atractomor-*

pha, although not in others. In many other genera, however, a spermathecal appendage is present, but not immediately obvious because it has migrated upwards to form an apical or subapical adjunct to one part or another of the principal seminal reservoir. The situation is often further obscured by the elongation and convolution of the parts involved and/or the development on them of secondary diverticula of various kinds. The homology of a subapical adjunct of the seminal reservoir with the spermathecal appendage is usually, but not always, clearly indicated by the presence of a small apical bulb.

The shift in position of the spermathecal appendage is most readily appreciated by reference to the tribe *Nereniini* (Kevan, 1966 g). In this tribe there are genera in which the appendage (which has an apical bulb) is in the primitive position of a secondary receptaculum seminis on the main spermathecal duct (low down in *Modernacris;* higher up in *Noonacris),* but in *Kapaoria,* an exactly comparable structure is found on the outer curve of the rather narrow spermathecal caecum (which is continuous with the spermathecal vesicle). In *Paratarbaleus* the appendage is apical (and the caecum very narrow), in *Fusiacris* and *Tarbaleopsis,* it has shifted very slightly further on to the inner curve of the caecum. The nature of the appendage is particularly clear in the last genus. *Paratarbaleus* is interesting in that it shows the beginnings of lobular secondary diverticula on the appendage. In *Megra* and *Nerenia* (referred to above as having a simple spermatheca), the whole receptaculum seminis is greatly elongated and convoluted, but from the position of the coils and the presence of a minute apical bulb it would seem that, in *Megra* at least, spermathecal duct, vesicle, caecum and appendage have all run together to form a continuous narrow tube. Other *Pyrgomorphidae* in which the spermathecal appendage has shifted to a subapical position without the complication of secondary diverticula include several genera of *Desmopterini (Desmoptera, Stenoxyphus, Stenoxyphellus, Stenxyphula)* — see, for example, Slifer (1940 a) and Kevan (1966 a). In this group the spermathecal vesicle and caecum are very narrow and ribbon-like, and the appendage very long, slender and convoluted. Similar are the *Chlorizeinini, Burmorthacris (Orthacridini,* the only genus of the tribe in which the spermathecal appendage is well formed), *Mekongiella (Sphenariini* — see Kevan, 1966 f — other members of this tribe have no spermathecal appendage), *Monistriini* (except for two genera with secondary diverticula as noted below; the spermathecal vesicle and

caecum are very narrow and the appendage very long), and *Taphronota (Taphronotini* — the other genus in the tribe, *Aularches,* has secondary diverticula).

As indicated above, there are also numerous genera with basically similar spermathecae to those just discussed, but with lobe-like or finger-like secondary diverticula. These secondary diverticula are found principally on the outer curve of the region representing the caecum of the spermatheca, although they may also extend to the lower parts of the spermathecal appendage. These genera include those *Desmopterini* not already referred to *(Doriaella* — see Kevan (1966 a) — and *Desmopterella,* in both of which the structures are very long and slender; *Menesesia* and *Menesesiella,* in which the parts are more normally proportioned), *Brunniella (Brunniellini), Greyacris* and *Cygniterra (Monistriini), Schulthessia (Schultessiini,* currently a subtribe of *Atractomorphini,* but should be regarded as a separate tribe), *Aularches (Taphronotini)* and all *Dictyophorini.*

This last tribe is especially noteworthy as the secondary diverticula range in form from a few small lobes, in *Maura,* to the most complex condition known in the *Orthoptera* (or perhaps in the whole *Insecta),* in *Dictyophorus.* In this last genus, both spermathecal appendage and caecum have numerous long, coiled, branching secondary diverticula (Slifer, 1940 a: pl. 3, fig. 23).

In conclusion one may quote Dirsh (1957) when he says: "All this indicates that the structure of the spermatheca [in the *Acridoidea* generally] cannot be used as a single taxonomic character, but sometimes it may be useful as an auxiliary one, though it must be used with due caution". Thus we have seen that different groups of *Acridoidea* may have characteristic spermathecae, and that many forms of spermatheca are characteristic for certain tribes of *Pyrgomorphidae.* It cannot, however, be argued that tribes having similar spermathecae are necessarily closely related, and we have several examples, notably the *Nereniini* and *Desmopterini,* in which several forms of spermatheca are found within tribes that are clearly homogeneous on other grounds.

5. Genitalic terminology in Pyrgomorphidae.

The following is an alphabetically arranged, annotated glossary of the genitalic terms adopted for the *Pyrgomorphidae* in the present work. Unless a term has been in continuous, general, unambiguous

use, the author(s) previously using it in its presently accepted sense (usually for *Acridoidea* other than *Pyrgomorphidae)* is (are) cited immediately following the term. Exceptions are made in the case of the present authors: to avoid repetition, if these authors used, but did not initiate, an accepted term, no reference to them is made. Synonymous or approximately equivalent terms and the authors using them (again largely for *Acridoidea* other than *Pyrgomorphidae)* are given after each definition. It may occasionally be that the homologies indicated are inaccurate due to difficulties of interpretation. Complete coverage of all the multifarious terms that have been used (or of all relevant literature) is not claimed; nor is any serious attempt made to establish or to adhere to priorities of usage. Most of the works published from the end of 1967 onwards are omitted as they were received only after the submission of the present paper for publication. They introduce no new terms of importance. References to terminology applied to homologous structures in insects other than *Acridoidea, s. str.,* are not included.

The male terminology here adopted has, for the most part, already been illustrated for *Pyrgomorphidae,* although without definition, by Kevan and Akbar (1963). A few additions and slight modifications have subsequently been made (Akbar and Kevan, 1964; Kevan, 1964 a, b, 1965, 1966 d-f, i; Kevan and Akbar, 1964; Kevan, Akbar and Singh, 1964; Kevan, Singh and Akbar, 1964 a, b; Akbar, 1966 b), the most significant being the substitution of 'apodemal plates' for 'apodemes' of the cingulum (Kevan and Akbar, 1964). This substitution, however, was not made by Kevan (1966 g) or by Akbar (1966 b). It may be noted that this last author refers to a number of terms as being new, but all had been published, if not defined, prior to the appearance of his paper. Most of the female structures have been referred to in the literature much less frequently than those of the male, and the terminology here adopted has been previously used only in part. Abbreviations used in the diagrams for various structures, both male and female, are listed on pp. 249-253). They will be used uniformly throughout these studies.

a) *The Male Structures.*

Aedeagal sclerites (Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Rehn and Eades, 1961 a-d ['ventral aedeagal sclerites', if stipulated]) — A pair of usually long and narrow, normally tapered,

sclerites extending from the endophallic apodemes to form the, usually larger, distal region of the endophallus; derived from the endophallic membrane *(Parameres* [or their main processes], Walker, 1922; MacGillivray, 1923; Hubbell, 1932; Else, 1934; Karandikar, 1942; *Ectoparameres,* Walker, 1922; Else, 1934; Karandikar, 1942; *Zubi, Zähne* or *Dentes,* Baranov, 1925; *Back valves of penis,* Boldyrev, 1929; *Valve inferior del pene,* Guarino, 1935; *Posterior (ventral) apical processes of aedeagus,* Snodgrass, 1935 b; *Lobi interni del pene,* Jannone, 1936; *Processi ventrali del pene,* Jannone, 1939; *Ventral valves of aedeagus,* Gurney, 1940; Roberts, 1941; Uvarov, 1948; Ander, 1956; Lal and Parshad, 1961 a, b; *Ventral penis valves,* Qadri, 1940; Albrecht, 1953; [ventral] *Aedeagal valves,* Roberts, 1941; Uvarov, 1943; *Styles copulateurs,* Grassé and Hollande, 1945, 1946; *Posterior* or *Apical process* [*of penis*], Ohmachi, 1950; *Ventral aedeagal valves,* Albrecht, 1956; Rehn and Grant, 1959 a; Kevan, 1967; *Apical valves of penis* [plus basal valves, in part], Dirsh, 1956, 1961, 1962, 1963 a-c, 1965 b, c, 1966 a, b; Barnum, 1959; Latif *et al.,* 1959; Uvarov, 1966; *Ventrale Valven,* Lux, 1957, 1961; *Penial valves* [apical plus basal], Hubbell, 1960; *Valva*[*s*] *del aedeagus* and *porción*[*es*] *basal*[*es*] *del aedeagus,* in part, Márquez Mayaudón, 1962; *Ventral valves of penis,* Thomas, 1963; *Apices of penis valves,* Jago, 1963; *Valves* and *Partie médiane plus apicale du pénis,* Descamps, 1966; *Partie apicale du pénis,* Descamps and Wintrebert, 1966 b; includes *Apical lobes of penis,* Uvarov, 1966). Division into apical and basal parts of the aedeagal sclerites is rare in *Pyrgomorphidae* and separated terms for these are not used here. In *Pyrgomorphidae,* also, the homology of the aedeagal sclerites with those of most other *Acridoidea* is not certain (see p. 185). The "ventral valves" of Karandikar (1942) refer to the ventral lobe of the ectophallus.

Aedeagal valves [*sensu stricto*] (Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Rehn and Eades, 1961 a-d ['ventral aedeagal valves', if stipulated]) — The normally rather poorly sclerotized, distal projecting lobes of the 'aedeagus' into which the apices of the aedeagal sclerites extend; partly ectophallic and partly endophallic in origin *(Prépuce,* in part, Peytoureau, 1895; Chopard, 1920 [not 1949 = *pallium*]; *Ventral lobes of penis,* in part, Walker, 1922; Else, 1934; Ohmachi, 1950; *Distal part of dorsal lobe of aedeagus,* in part, Snodgrass, 1935 a, 1935 b; *Sheath of aedeagus,* in part, Roberts, 1941; Lal and Parshad, 1961 a, b; *Sheath (of penis),* in part, Dirsh, 1956, 1961,

1962, 1965 b, 1966 a, b; Barnum, 1959; *Sheath of aedeagal valves,* in part, Rehn and Grant, 1959 b; *Proceso*[*s*] *apicales del aedeagus,* in part, Márquez Mayaudón, 1962 [includes also apices of aedeagal sclerites?]. *Lateral appendices of penis valves,* Jago, 1963; *Sheath of apex of penis,* Dirsh, 1965) — see also under 'Sheaths of ectophallus'. For 'dorsal' and 'ventral aedeagal valves' of other authors, see 'Valves of cingulum' and 'Aedeagal sclerites'.

Aedeagus (MacGillivray, 1923; Else, 1934; Snodgrass, 1935 a, b, 1937; Qadri, 1940; Roberts, 1941; Uvarov, 1943, 1948; Grassé and Hollande, 1945, 1946; Albrecht, 1953, in part, 1956, in small part; Ander, 1956; Dirsh, 1956, in part; Gurney and Eades, 1961 — The distal parts of the endophallic sclerites which act as the chief intromittant organ; a term of convenience only as the structures are not homologous with the aedeagus of non-orthopteroid insects; the term, if used at all for orthopteroids should perhaps more properly be used for the whole of the distal part of the phallus, not just for the endophallic parts (Eades, 1961 b) *(Penis,* Brunner von Wattenwyl, 1876; Packard, 1878; Walker, 1922; MacGillivray, 1923; Fedorov, 1927, in part, Znoĭko, 1928; Boldȳrev, 1929; Nel, 1929; Hubbell, 1932; Else, 1934, in part; Snodgrass, 1935 a, in part; Uvarov, 1948; Thomas, 1963; *Uncini* or *Uncus,* Berlese, 1882; *Partie libre du pénis,* Peytoureau, 1895; *Upper end of penis,* Snodgrass, 1903; *Organo copulatore,* in part, Berlese, 1906; *Pénis,* Chopard, 1920, 1949; *"Lancette" of penis,* Fedorov, 1927; *Pene,* Silvestri, 1934; Jannone, 1936, 1937; *Cylindrical distal part* [*of penis*], Ohmachi, 1950; *Median intromittant part of aedeagus,* Albrecht, 1953; *Phallushaken,* Beier, 1955; *Intromittant organ,* Albrecht, 1956.

Ancorae (or *Anterior* or *Ventral hook-like processes,* or *Cornua, of epiphallus)* — Not present in *Pyrgomorphidae* (see p. 177).

Anterior projections (of epiphallus) (Dirsh, 1956, 1963 b, 1965 b, 1966 b) — A pair of laterally situated, lobe-like, or sometimes elongate, projections on the anterior margins of the lateral plates of the epiphallus *(Expansions carrées de la pièce transversale,* Peytoureau, 1895; *Processi laterales epiphalli,* Ander, 1956; *Anterior processes,* Barnum, 1959; Akbar, 1966 a [figure only]; *Ancorae* [erroneously], Dirsh, 1959, 1963 b [*Chapmanacris* and *Pyrgohippus* only]; *Lateral projections of epiphallus,* Dirsh, 1963 b [*Dyscolorhinus* only]; *Projections antérieures (de l'épiphalle),* Descamps, 1966; Descamps and Wintre-

bert, 1966 b; *Antero-lateral projections,* Akbar, 1966 a [also uses accepted term]).

Apical aedeagal sclerites — see 'Aedeagal sclerites'.

Apodemal plates (of cingulum) (Kevan and Akbar, 1964) — Large, paired, convex, lobe-like structures forming the anterior, sclerotized parts of the pyrgomorphid cingulum *(Apodemes [of cingulum],* Roberts, 1941, in part; Dirsh, 1956, in part; Latif *et al.,* 1959; Kevan and Akbar, 1963; Akbar and Kevan, 1964; Kevan, Akbar and Singh, 1964; Kevan, Singh and Akbar, 1964 a; Kevan, 1966 g; Akbar, 1966 b; *Plaques apodémales,* Descamps and Wintrebert, 1966 b).

Apodemes (of cingulum) (Roberts, 1941; Uvarov, 1943; Ander, 1956; Dirsh, 1956, 1961, 1962, 1963 a-c, 1965 a-c, 1966 a, b; Barnum, 1959; Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Lal and Parshad, 1961 a, b; Rehn and Eades, 1961 a-d; Kevan and Akbar, 1964; Uvarov, 1966) — A pair of usually large rod-like, sometimes plate-like, normally dorsolateral, sclerites forming the anterior part of the cingulum; in *Pyrgomorphidae* apparently represented only in some forms by small anteroventral processes of the apodemal plates — see Ventral processes of apodemal plates' and p. 180 — *(Chitinisation laterale de la région interne du pénis,* Peytoureau, 1895; *Epifallo,* in part, Berlese, 1906 [not the epiphallus]; *Apophyses du pont,* Chopard, 1920; *Endapophyses,* Walker, 1922; Hubbell, 1932; Qadri, 1940; *Elongate grooved plates,* MacGillivray, 1923; *Vilitsa, Gabel,* or *Furca,* Baranov, 1925; *Epiphyses pontis posterioris,* Znoĭko, 1928; *Endopophyses,* Else, 1934; *Bracci di leva del pene,* Silvestri, 1934; Jannone, 1936; *Apodemes,* Snodgrass, 1935 b; Albrecht, 1956; *Apodemi a ferro di cavallo del pene,* Jannone, 1937; *Apodemi del pene,* Jannone, 1939; *Apophyses (of dorsal valve),* Karandikar, 1942; *Apophyses latérodorsales de la pièce tegulaire,* Grassé and Hollande, 1945; *Aedeagal apodemes,* Albrecht, 1953, 1956; Thomas, 1963; *Apodemen,* Lux, 1957, 1961; *Apodema(s) del cingulum,* Márquez Mayaudón, 1962; *Cingular apodemes,* Jago, 1963; *Apodemi* [in singular, 'Apodemus'], Dirsh, 1965 c; *Apodèmes,* Descamps, 1966; Descamps and Wintrebert, 1966). The "apodeme" of Karandikar (1942) refers to part of the ectophallic membrane.

Apodemes of endophallus — See 'Endophallic apodemes'.

Appendices (of epiphallus) (Kevan and Akbar, 1963, 1964; Akbar, 1966 b) — In *Pyrgomorphidae,* paired, elongate, rarely plate-like, usually club-like sclerites with basal stalks and distal lobes (that may

have terminal processes), articulating marginally or submarginally with the lateral plates or the anterior projections of the epiphallus; characteristic for *Pyrgomorphidae;* of different form when present in other families; possibly representing the styli of the vestigial tenth sternum (see p. 176) (? *Plaques carrées,* Peytoureau, 1895; *Oval sclerites,* Snodgrass, 1935 b; Albrecht, 1953, 1956; Dirsh, 1956, 1961, 1965 b, c, 1966 b; Eades, 1961 a, 1963; Rehn and Eades, 1961 a, c, d; Jago, 1963; Kevan, 1966 g; *Piccolo pezzo libero,* Guarino, 1935; *Lateral sclerites (of epiphallus),* Roberts, 1941; Karandikar, 1942; Ander, 1956; Barnum, 1959; *Dorso-lateral appendices of epiphallus* [unlike other terms, applied specifically to *Pyrgomorphidae*], Dirsh, 1956, 1961, 1963 b, 1965 b, 1966 b; Latif *et al.,* 1959; Akbar, 1966 a, b; Uvarov, 1966; *Proceso*[*s*] *lateral*[*es*] *del epiphallus,* Márquez Mayaudón, 1962; *Smaller sclerites,* Thomas, 1963; *Appendices dorso-latéraux* [or *Sclérites ovales* in Acrididae] *de l'épiphalle,* Descamps and Wintrebert, 1966 b).

Arch of cingulum (or of 'dorsal valves' or of 'aedeagal valves') or *Ponticulus* — Not present in *Pyrgomorphidae,* but see Pseudoarch.

Basal aedeagal sclerites — See 'Aedeagal sclerites'.

Basal emargination (of cingulum) (Kevan and Akbar, 1962, 1964). — A U- or V-shaped dorsal excavation of the anterior margin of the cingulum between the apodemal plates; rarely virtually absent; occasionally greatly exaggerated.

Basal fold (of ectophallic membrane) (Snodgrass, 1935 b; Roberts, 1941; Albrecht, 1953, 1956; Ander, 1956; Dirsh, 1956, 1961; Barnum, 1959; Hubbell, 1960; Eades, 1961 a, b, 1962; Gurney and Eades, 1961; Lal and Parshad, 1961 a, b; Rehn and Eades, 1961 a-d; Thomas, 1963) — A fold formed by the posterior part of the membrane over the distal, dorsal part of the cingulum; sometimes partially sclerotized to form a 'hood' *(q. v.)* (? *Glande* or *Glans,* in part, Berlese, 1882; *Zone membraneuse,* Grassé and Hollande, 1945; *Dorsal fold,* Dirsh, 1956; Hubbell, 1960; Rehn and Grant, 1960 b; *Basalfalte,* Lux, 1957, 1961).

Basal thickening (of cingulum) (Kevan and Akbar, 1963, 1964; Akbar, 1966 b) — The strongly sclerotized, anterior margins of the cingulum (dorsal and lateral) running around the basal emargination and the proximal parts of the apodemal plates; dorsal part sometimes in the form of a rather wide, collar-like plate lying beneath the anterior region of the suprazygomal plate; mainly a strengthening ridge.

Bridge of cingulum — Not recognized in *Pyrgomorphidae.*

Bridge (of epiphallus) (Snodgrass, 1935 b, Gurney, 1940; Roberts, 1941; Albrecht, 1953; Dirsh, 1956, 1961, 1962, 1963 b, 1965 b, c, 1966 a, b; Barnum, 1959; Latif *et al.*, 1959; Hubbell, 1960; Rehn and Eades, 1961 b-d; Vickery, 1967 a) — The median sclerotized part of the epiphallus connecting the lateral plates; occasionally undifferentiated from the latter *(Pièce transversale,* in part, Peytoureau, 1895; *Barette transversale,* Chopard, 1920; *Dura, Bogen* or *Arca* [of supragenital sclerite], Baranov, 1925; *Arcus,* Znoĭko, 1928; Ander, 1956; Márquez Mayaudón, 1962 [only the more heavily sclerotized part]; *Transverse bar of pseudosternite,* Hubbell, 1932; *Ponte dell'epifallo,* Jannone, 1939; *Medium* of *Median sclerite,* Karandikar, 1942; *Transverse bridge of epiphallus,* Albrecht, 1953; *Arc,* Ander, 1956; *Median bridge,* Lal and Parshad, 1961 a, b; *Pliegue basal del Phallus,* Márquez Mayaudón, 1962 [only the membranous porterior part]; *Disque de l'épiphalle,* Descamps and Wintrebert, 1966).

Central membrane of ectophallus (Kevan and Akbar, 1963; 1964; Akbar, 1966 b) — The unsclerotized area on the dorsal surface of the ectophallus, lying between the zygoma and the rami of the cingulum; not regarded as being truly part of the cingulum, but pertaining to the ectophallic membrane *(Face supérieure de la partie intra-abdominale du pénis,* in part, Peytoureau, 1895; *Membrana dorsale,* Jannone, 1939; *Basal eminence* or *Summit of zygoma,* Hubbell, 1960; *Central membrane,* Eades, 1961 a; Gurney and Eades, 1961; *Central membrane of cingulum,* Eades, 1961 b, 1962; Kevan, 1966 b, g; *Membrane of cingulum,* Kevan, 1964 b; *Membrane centrale (du cingulum),* Descamps and Wintrebert, 1966 b).

Cingulum (Roberts, 1941; Uvarov, 1943; Chopard, 1949 [incorrectly attributed to Snodgrass]; Albrecht, 1956; Ander, 1956; Dirsh, 1956, 1961, 1962, 1963 a-c, 1965 b, c, 1966 a, b; Rehn and Grant, 1958, 1960; Latif *et al.*, 1959; Hubbell, 1960; Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Rehn and Eades, 1961 a-d; Jago, 1963; Rehn and Randell, 1963; Descamps, 1966; Descamps and Wintrebert, 1966 b; Uvarov, 1966 [all in part (central membrane of ectophallus included)] — In *Pyrgomorphidae,* a capsule-like, sclerotized structure surrounding the endophallus and incorporating the apodemal plates, zygoma, suprazygomal plate (if present), rami, suprarami (if present), sheaths (usually in part only) and sometimes an inflection of the pseudoarch or certain special sclerotizations, but not the central membrane of the ectophallus *(Prepuzio,* approximately, Berlese, 1882; *Partie intra-*

abdominale du pénis, approximately, Peytoureau, 1895; *Lateral projections of brachiae,* approximately, MacGillivray, 1923; *Apodemi del pene,* Jannone, 1939; *Dorsal valve, Dorsal valvular sclerite* or *collar-like structure,* Karandikar, 1942; *Tégule* or *Tegula,* Grassé and Hollande, 1945; *Pièce tégulaire,* Grassé and Hollande, 1945, 1946; *Broad proximal part* [*of aedeagus*], Ohmachi, 1950; *Tegula,* Ander, 1956).

Cingulum valves — See 'Valves of cingulum'.

Dorsal cleft (of cingulum) (Kevan and Akbar, 1963, 1964; Akbar, 1966 b) — The dorsal, distal opening of the phallotreme, continuous with the ventral cleft *(q. v.);* formed by the union of the fused ecto- and endophallic membranes along the inner margins of the sheaths of the ectophallus *(Phallotreme cleft,* in part, Snodgrass, 1935 b; *Dorsal phallotreme cleft,* Eades, 1961 b; Gurney and Eades, 1961; Rehn and Eades, 1961 b).

Dorsal inflections (of endophallic apodemes) (Kevan and Akbar, 1963, 1964; Kevan, 1966 h; Akbar, 1966 b) — Inwardly directed dorsal expansions of the bases of the endophallic sclerites (apodemes); when present, usually partly covering the spermatophore sac.

Dorsal processes of aedeagal valves — Strongly sclerotized lateral adjuncts of the pseudoarch arising from the aedeagal valves, as in *Schulthessia (Dorsal appendices of penis,* in part, Dirsh, 1956).

Dorsal transverse ridge of cingulum — A transverse sclerotization in the posterior part of the zygoma of *Gymnohippini* and some *Desmopterini (Sclérification transverse limitant à l'avant la membrane centrale du cingulum,* Descamps and Wintrebert, 1966 b).

Ectophallic membrane (auctt.) — A double-layered membrane derived from the ectoderm, largely enveloping the cingulum, forming the basal fold and lateral lobes, and continuing antero-ventrally to form the ventral infold; also, strictly, includes the central membrane of the ectophallus, the valves of the cingulum, the pseudoarch and parts of the sheaths and aedeagal valves *(Membrana,* Berlese, 1882; *Membrane,* Peytoureau, 1895; *Genatasinus,* MacGillivray, 1923; *Genitosinus,* Else, 1934; *Manicotto subprossimale del pene,* Jannone, 1937; *Intersegmental membrane,* in part, and *(Membranous) apodeme,* Karandikar, 1942; *Membranes périphalliques,* Grassé and Hollande, 1946; *Phallic membrane,* Ander, 1956; *Membrana ectophallica,* Márquez Mayaudón, 1962; *Membrane ectophallique,* Descamps, 1966; *Ectophallus membrane* [*lapsus* in one place] Dirsh, 1966 a). The 'area inferior' of the epiphallus of Znoĭko (1928) seems to represent part of this membrane.

Ectophallus (auctt.) — The phallic structures other than the epiphallus and endophallus and their associated membranes *(Praeputium,* Packard, 1878; *Ectophalle,* Descamps and Wintrebert, 1966 b).

Ejaculatory duct (auctt.) — The terminal part of the vessel conveying the genital products from the gonads to the endophallus *(Ductus ejaculatorius,* Packard, 1878; Snodgrass, 1903; Fedorov, 1927; Boldȳrev, 1929; Beier, 1955; Lux, 1957, 1961; *Canale eiaculatore,* in part, Berlese, 1882; *Conduit génital,* Peytoureau, 1895; [include] *seminal duct of penis,* Snodgrass, 1903; *Condotto eiaculatore,* Silvestri, 1934; *Condotto ejaculatore,* Jannone, 1936, 1937, 1939; *Canal ejeculateur,* Grassé and Hollande, 1945, 1946; Chopard, 1949; Descamps, 1966; Descamps and Wintrebert, 1966 b).

Ejaculatory sac (auctt.) — A large endophallic vesicle formed by the widening of the ejaculatory duct (situated, in *Pyrgomorphidae,* ventrally to the aedeagal sclerites) and communicating with the spermatophore sac through the gonopore; opening distally along the ventral cleft *(Spermatic pouch,* Snodgrass, 1903; *Saccus,* Boldȳrev, 1929, *Sacco ejaculatore,* Jannone, 1937, 1939; *Sac ejaculateur,* Grassé and Hollande, 1945, 1946; Chopard, 1949; Descamps, 1966; Descamps and Wintrebert, 1966 b); *Sacculus ejaculatorius,* Lux, 1957, 1961; *Endophallic sac(s),* in part, Jago, 1963; Dirsh, 1966 b).

Endophallic apodemes (Eades, 1961 a, 1962; Gurney and Eades, 1961; Rehn and Eades, 1961 a-d) — The basal, expanded parts of the endophallic sclerites *(Os penis,* Berlese, 1882; *Apophyses antérieurs,* Peytoureau, 1895; *Ipofallo,* Berlese, 1906; *Valves génitales supérieures,* Chopard, 1920; *Endoparameres,* Walker, 1922; Hubbell, 1932; Else, 1934; Qadri, 1940; Karandikar, 1942; *Bases of parameres,* Walker, 1922; *Parademes* MacGillivray, 1923; *"Shell" of penis,* in part, Fedorov, 1927; *Paramere bases,* Hubbell, 1932; *Krili, Flügel* or *Alae,* Baranov, 1925; *Valvae superiores,* Znoĭko, 1928; Boldȳrev, 1929; *Aedeagal apodemes,* Snodgrass, 1935 a; Kevan, 1966 h; *Anterior apodemes of endophallic plates,* Snodgrass, 1935 b; *Apodemi anterior delle lamina endofallici,* Jannone, 1937, 1939; *Endophallic plates,* approximately, Roberts, 1941; Uvarov, 1948; Albrecht, 1953, 1956; Ander, 1956; Rehn and Grant, 1959 a-c; Lal and Parshad, 1961 a, b; Rehn and Randell, 1963; Thomas, 1963; Kevan, 1967; *Laminae penis,* in part, Grassé and Hollande, 1945, 1946; *Plaques endophalliques* and *Alae penis,* Chopard, 1949 [latter attributed to Berlese]; *Upper genital valves,* Ohmachi, 1950; *Apodemen* [*des Endophallus*], Beier, 1958; *Laminae*

phalli, Ander, 1956; *Basal plates* [*of penis*], Dirsh, 1956; *Basalplatten,* Lux, 1957, 1961; *Basal valves of penis,* in part, Barnum, 1959; Latif *et al.,* 1959, Dirsh, 1961, 1962, 1963 a-c, 1965 b, c, 1966 a, b; *Gonopore processes,* in part [erroneously], Barnum, 1959; *Basal penial valves,* Hubbell, 1960; *Porcion*[*es*] *basal*[*es*] *del aedeagus,* in part, Márquez Mayaudón, 1962; *Internal anterior expansions of penis valves,* Jago, 1963; *Partie basale (au pénis),* Descamps, 1966; Descamps and Wintrebert, 1966 b).

Endophallic membrane (Ander, 1956; Dirsh, 1956; Eades, 1961 b) — The unsclerotized parts of the endophallus; continuous with ectophallic membrane *(Khimenozni deo, Häutiger Teil* or *Pars hymenosus,* Baranov, 1925).

Endophallic sclerites (Roberts, 1941; Ander, 1956; Dirsh, 1956, 1966 b) — The sclerotized parts of the endophallus, comprising the endophallic apodemes [basal] and the aedeagal sclerites [apical] *(Sword-shaped projections* [*of brachiae*], MacGillivray, 1923; *Trup, Körper* or *Corpus,* approximately, Baranov, 1925; *Endofallo,* Jannone, 1939; *Aedeagus,* Qadri, 1940; Lux, 1957, 1961; Rehn and Randell, 1963; Uvarov, 1966; *Laminae penis,* Grassé and Hollande, 1945, 1946; *Oedeagus* Chopard, 1949; *Penis,* Dirsh, 1956, 1961, 1962, 1963 a-c, 1965 b, c, 1966; Lux, 1957, 1961; Uvarov, 1966; *Penis valves,* Jago, 1963; Uvarov, 1966; *Pénis,* Descamps, 1966; Descamps and Wintrebert, 1966 b).

Endophallus (auctt.) — The internal parts of the phallic complex, comprising the endophallic sclerites and membrane, the spermatophore sac, the ejaculatory sac and parts of the aedeagal valves *(Chitinous centre of penis,* Snodgrass, 1903; *Fallo,* Berlese, 1906; *Penis,* Fedorov, 1927; Ohmachi, 1950; *Penial apparatus,* Karandikar, 1942; Vickery, 1967 a; *Aedeagus,* Karandikar, 1942; Albrecht, 1956, *Pénis,* Grassé and Hollande, 1945; *Endophalle,* Descamps and Wintrebert, 1966 b).

Ephiphallic infold (Eades, 1961 a, b; Rehn and Eades, 1961 a-d) — An invagination of the ectophallic membrane lying anterior to the epiphallus *(Bourrelet membranea médian,* Peytoureau, 1895). Limits the *Supra-genital cavity* of Karandikar (1942).

Epiphallus (Crampton, 1918; Znoĭko, 1928; Boldyrev, 1929, Snodgrass, 1935 a, b; Qadri, 1940; Roberts, 1941; Karandikar, 1942; Uvarov, 1943, 1948; Ohmachi, 1950; Albrecht, 1953, 1956; Beier, 1955; Ander, 1956; Dirsh, 1956, 1961, 1962, 1963 a-c, 1965 b, c, 1966 a, b; Lux, 1957, 1961; Rehn and Grant, 1958, 1959 a-c, 1960 a-c; Barnum,

1959; Latif *et al.*, 1959; Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Márquez Mayaudón, 1962; Rehn and Eades, 1961 a-d; Jago, 1963; Rehn and Randell, 1963; Thomas, 1963, 1965; Uvarov, 1966; Vickery, 1967 a) — A strongly sclerotized structure of characteristic form, situated dorsally to the cingulum, to which it is connected by a membrane; possibly homologous with the tenth abdominal sternum, or part of it *(Titillator,* Brunner von Wattenwyl, 1876; Crampton, 1918; Znoĭko, 1928; Boldȳrev, 1929; *Uncinietti* or *Unguiculae penis,* Berlese, 1882; *Pièce transversale, sens. lat.,* Peytoureau, 1895; *Vertical, transverse, chitinous plate* or *Plate in genital chamber before base of penis,* Snodgrass, 1903; *Altro sclerite del perifallo,* Berlese, 1906; *Epihamulus,* Crampton, 1918; *Epiphalle,* Chopard, 1920, 1949; Grassé and Hollande, 1945, 1946; Descamps, 1966; Descamps and Wintrebert, 1966 b; *Titillateur* or *Pont antérieur,* Chopard, 1920; *Pseudosternite,* Walker, 1922; MacGillivray, 1923; Hubbell, 1932; Else, 1934; Chopard, 1949; Ohmachi, 1950; *Peronea,* MacGillivray, 1923; *Epifallo,* Guarino, 1935; *Pseudosternum,* Qadri, 1940; *Clasper,* Ohmachi, 1950; *Pseudosternit,* Beier, 1955). Note that 'epifallo' of Berlese (1906) refers to a different part of the phallic complex, apparently the apodemes of the cingulum together with the zygoma. 'Titillator', as a synonymous term, as indicated above, is defined by Snodgrass (1935 a) for insects generally, as a terminal process of the aedeagus; it is thus ambiguous and should be avoided.

Externolateral expansions of lateral plates (or epiphallus) (Kevan and Akbar, 1964; Akbar, 1966 b) — Laminae, usually somewhat triangular in shape, projecting posterolaterally from the external margins of the lateral plates of the epiphallus (of which they form an integral part); characteristic of subtribe *Pyrgomorphina,* but also found elsewhere *(Lateral, angular propections,* Kevan, 1966 e). These may be homologous with the 'Posterior projections of the epiphallus' (q. v.) of other *Acridoidea.*

Flexure (of aedeagal sclerites) (Roberts, 1941; Dirsh, 1956, 1961, 1962, 1965 b, c, 1966 a, b; Barnum, 1959; Descamps, 1966; Uvarov, 1966) — The narrow, weak connection (sometimes broken) between the basal and apical aedeagal sclerites; characteristic of *Acrididae,* but rare and possibly not homologous in *Pyrgomorphidae (Sigmoid flexure,* Snodgrass, 1935 b; *Courbure sigmoïde (des laminae penis),* Grassé and Hollande, 1945; Ander, 1956; *S-shaped bend of ventral penis valve,* Albrecht, 1953; *Sigmoid flexure of the ventral aedeagal valve,* Albrecht,

1956; *Sigmoid bow,* Ander, 1956; *S-förmige Schleife,* Lux, 1957, 1961; *Flexible bend,* Hubbell, 1960; *Flexure* [*Acrididae*] or *Suture subterminale* [*Pyrgomorphidae*], Descamps and Wintrebert, 1966; *Articulation,* Dirsh, 1966 b).

Genital chamber (auctt.) — A cavity at the apex of the abdomen lodging the phallic complex, bounded chiefly by the epiproct or supra-anal plate (11th abdominal tergum), paraprocts and subgenital plate (9th abdominal sternum) *(Cavité supragénital,* Chopard, 1920; *Ninth sternal cavity,* Else, 1934; *Chambre génitale,* Grassé and Hollande, 1945; *Genitaltasche,* Beier, 1955; *Genitalkammer,* Lux, 1957, 1961).

Gonopore (Walker, 1922; Snodgrass, 1935 a, b; Roberts, 1941; Grassé and Hollande, 1945; Ander, 1956; Dirsh, 1956; Barnum, 1959; Uvarov, 1966) — A short, transverse, slit-like passage connecting the ventral part of the spermatophore sac with the ejaculatory sac; this is the true or primary gonopore.

Gonopore process of endophallus — Not present in *Pyrgomorphidae,* unless the aedeagal sclerites of this family are, in part, derived from them (see p. 185).

Hood (of ectophallus) (Kevan and Akbar, 1964; Kevan, 1965, 1966 d) — A sclerotized development of the ectophallic membrane dorsal to, or surrounding the posterior part of the cingulum; sometimes incorporating much of the lateral lobes or special rod-like or plate-like areas; peculiar to *Fijipyrgini, Mitricephalini* and *Geloiini.* The "hood" of Boldyrev (1929) is the upper part of the pallium *(q. v.).*

Inflections of rami (of cingulum) (Kevan, Singh and Akbar, 1964 b) — A pair of posterior, flap-like structures originating from the rami or suprarami; when present, varying considerably in size and shape *(Ramal inflections,* Kevan and Akbar, 1963; *Supraramal inflections,* Kevan, 1964 b; *Inflections of suprarami,* Kevan, 1966 f; ? *Épaisses saillies,* Descamps, 1966).

Lateral lobes (of ectophallic membrane) (Roberts, 1941; Ander, 1956; Eades, 1961 a, b; Rehn and Eades, 1961 a-d; Dirsh, 1963 b) — A pair of lobes formed by the ectophallic membrane, lying laterally to the cingulum and joined basally at or near the ventral, proximal parts of the rami *(Poches latéro-apicales,* Descamps, 1966).

Lateral oblique thickenings (of the cingulum) (Kevan, Singh and Akbar, 1964 b) — A pair of sclerotized bands running backwards along the sides of the cingulum from ventral, posterior extensions of the basal thickening.

Lateral plates of endophallic sclerites — Not present as such in *Pyrgomorphidae* (see p. 185).

Lateral plates (of epiphallus) (Roberts, 1941 [who used it in a narrower sense]: Dirsh, 1956, 1961, 1965 b, c, 1966 a, b; Barnum, 1959; Latif *et al.*, 1959; Rehn and Eades, 1961 b) — A pair of (usually) elongate plates forming the two sides of the epiphallus and connected by the bridge; sometimes extended laterally to form externolateral expansions *(q. v.) (Rebords externes de la pièce transversale,* Peytoureau, 1895; *Pièces verticales,* Chopard, 1920; *Plochitsi, Platten* or *Alae* [of supragenital sclerite], Baranov, 1925; *Laminae laterales (epiphalli),* Znoĭko, 1928; Ander, 1956: *Prolungamenti verticali* [*del epifallo*], Guarino, 1935; *Lateral lobes,* Snodgrass, 1935 b; Albrecht, 1953, 1956; *Lobi laterali dell'epifallo,* Jannone, 1939).

Lophi (of epiphallus) (Roberts, 1941; Ander, 1956; Dirsh, 1956 [except *Pyrgomorphidae*], 1959, 1961, 1962, 1963 a-c, 1965 b, c, 1966 a, b; Barnum, 1959; Rehn and Grant, 1959 a, b; Lal and Parshad, 1961 a, b; Rehn and Eades, 1961 a-d; Márquez Mayaudón, 1962 [includes also thickened parts of lateral plates]; Rehn and Randell, 1963; Descamps and Wintrebert, 1966 b) — A pair of strongly sclerotized, usually hook-like, processes arising from the posterior ends of the lateral plates of the epiphallus ([*due*] *Uncinietti* or *Unguiculae penis* [*diretti indietro*], Berlese, 1882; *Rebords postérieurs de la pièce transversale,* Peytoureau, 1895; [posterior] *Hook-like process*[*es*], Snodgrass, 1903; *Postcornua* or *Processes of pseudosternite,* Walker, 1922; *Izrashtay, Vorsprünge* or *Squamae* [of supragenital sclerite], Baranov, 1925; *Lobi papillati,* in part, comprising *pars posterior* and *pars anterior,* Znoĭko, 1928; *Depressors,* Boldyrev, 1929; *Dorsal lobes of pseudosternite,* Hubbell, 1932; *Transverse* or *Posterior processes of epiphallus,* Snodgrass, 1935 b; *Processi posteriori dell'epifallo,* Jannone, 1939; *Dorsal lobes (of epiphallus),* Karandikar, 1942; [posterior] *Hook-like processes of epiphallus,* Albrecht, 1953, 1956; *Posterior projections (of epiphallus),* Dirsh, 1956 [in *Pyrgomorphidae*], Latif *et al.*, 1959; *Ohrenförmige Höcker,* Lux, 1957, 1961; *Parte*[*s*] *apical*[*es*] or *Porción*[*es*] *distal*[*es*] *del lophi,* Márquez Mayaudón, 1962; *Hooks of epiphallus,* Thomas, 1965).

Median projection of epiphallus (Dirsh, 1956; Latif *et al.*, 1959) — A short, median lobe sometimes present on the anterior (or posterior) margin of the bridge *(Median process of epiphallus,* Akbar, 1966 b; *Frontal projection* [*of epiphallus*], Vickery, 1967 a).

Oval sclerites of epiphallus — See 'Appendices of epiphallus'.

Pallium (Walker, 1922; Else, 1934; Snodgrass, 1935 b; Roberts, 1941; Karandikar, 1942; Grassé and Hollande, 1945; Uvarov, 1948; Ohmachi, 1950; Albrecht, 1953; Beier, 1955; Ander, 1956; Dirsh, 1956; Lux, 1937, 1961; Barnum, 1959; Eades, 1961 a, 1962; Rehn and Eades, 1961 a-c; Thomas, 1963, Uvarov, 1966) — A continuation of the ectophallic membrane joining the phallus with the posterior parts of the subgenital plate *(Obere Haut der Lamina subgenitalis,* Brunner von Wattenwyl, 1876; *Velum penis,* Packard, 1878; *Cappuccio,* Berlese, 1882, 1906; *Puppis* or *Prora,* Crampton, 1918; *Capuchon inférieur,* Chopard, 1920; *Decacoria,* MacGillivray, 1923; *Hood,* Boldyrev, *Cappuccetto membranoso,* Guarino, 1935; *Membrana scrotale,* Jannone, 1939; *Pallial membrane,* Karandikar, 1942; *Prépuce,* Chopard, 1949 [not 1920 = Aedeagal valves in part].

Phallic complex (Dirsh, 1956, 1961, 1962, 1963 a-c, 1965 b, c, 1966 a, b; Albrecht, 1956; Barnum, 1959; Eades, 1961 a, 1962; Gurney and Eades, 1961; Rehn and Eades, 1961 a-d; Jago, 1963; Uvarov, 1966) — The epiphallus, ectophallus and endophallus, together with their associated membranes *(Penis,* approximately, Brunner von Wattenwyl, 1876; Comstock and Kellogg, 1899; *Armature génitale,* Peytoureau, 1895; *Pene,* Berlese, 1882; *Organi copulatori,* Berlese, 1906; *Genitalia, s. str.,* MacGillivray, 1923; Karandikar, 1942; *Kopulatsioni aparat,* Baranov, 1925; *Eigentlicher Kopulationsapparat,* Baranov, 1925; Lux, 1957, 1961; *Secondary internal genitalia,* Else, 1934; *Phallic organs* Snodgrass, 1935 b; *Phallic structures,* Roberts, 1941; Eades, 1961 a, b, 1962, 1963; Rehn and Randell, 1963; Kevan, 1966 h; *Phallus,* Beier, 1955; Hubbell, 1960; *Copulatory organ,* Albrecht, 1956; *Complexe phallique,* Descamps, 1966; Descamps and Wintrebert, 1966 b).

Phallic organ and *Phallic organs* — see 'Phallus' and 'Pallic complex' respectively.

Phallotreme (Snodgrass, 1935 a, b; Roberts, 1941; Uvarov, 1943; Dirsh, 1956, 1961; Barnum, 1959; Latif *et al.,* 1959; Hubbell, 1960; Eades, 1961 a, b, 1962; Lal and Parshad, 1961 a, b; Rehn and Eades, 1961 b; Thomas, 1963, all in part) — The ventral, longitudinal, slit-like opening between the distal parts of the endophallic sclerites, extending from the gonopore to the apices of the aedeagal valves *(Canale eiaculatore,* in part, Berlese, 1882; *Genital opening,* Snodgrass, 1903; Karandikar, 1942; *Opening of penis,* Fedorov, 1927; *Phallotreme cleft,* in

part, Snodgrass, 1935 b; *Fente phallotrémique,* in part, Grassé and Hollande, 1945, 1946; *Phallotrème,* Chopard, 1949; Descamps, 1966; *Pallotrema,* Ander, 1956; *Phallotremer Spalt,* Lux, 1957, 1961; *Endophallic sac(s),* in part, Jago, 1963; Dirsh, 1966 b).

Phallotreme duct (Roberts, 1941; Uvarov, 1943; Ander, 1956) — The narrow, distal extension of the spermatophore sac which dorsally unites the aedeagal sclerites; the phallotreme lies below it *(Phallotreme* and synonymous terms of authors cited above as 'in part'; *Meatus,* approximately, MacGillivray, 1923; Snodgrass, 1935 b; *Troughlike passage,* Karandikar, 1942).

Phallus [*sensu stricto*] (Crampton, 1918; Snodgrass, 1935 a, b; Roberts, 1941; Chopard, 1949; Albrecht, 1956; Ander, 1956; Dirsh, 1956, Latif *et al.,* 1959; Eades, 1961 b, 1963) — The phallic complex without the epiphallus and its associated membranes *(Pénis,* Peytoureau, 1895; *Penis,* Snodgrass, 1903; *True penis,* Crampton, 1918; *Brachiae,* approximately, MacGillivray, 1923; *Kopulatsioni organ* or *Kopulationsorgan,* Baranov, 1925; *Kopulyativïi apparat,* Znoĭko, 1928; *Genital mass,* Hubbell, 1932; *Copulatory apparatus,* Else, 1934; *Pene,* Guarino, 1935; *Appareil* or *Organe copulateur,* Grassé and Hollande, 1945, 1946; *Aedeagus,* Ohmachi, 1950; Márquez Mayaudón, 1962). The *Phallus body* of Ander (1956), or *Phallobasis* of Lux (1957, 1961), excludes the 'aedeagus', but apparently not the rest of the endophallus.

Posterior inflections of cingulum — A pair of sclerotized processes joining the bases of the valves of the cingulum or pseudoarch with the posterior parts of the rami (*"PZI"* [undefined], Kevan and Akbar, 1964; *Processi sclérifiés réunissants les valves du cingulum aux expansions postéro-ventrales des rami,* Descamps and Wintrebert, 1966 b; *Inflection* [*of pseudoarch*], Akbar, 1966 b).

Posterior processes of epiphallus — Lobe-like continuations of the lateral plates extending a short distance beyond the lophi; peculiar to *Pseudomorphacridini;* presumably not homologous with the posterior projections of the epiphallus *(q. v.).* The structures called 'posterior processes of the epiphallus' by Snodgrass (1935 b) are the lophi *(q. v.);* those of Barnum (1959) and Rehn and Randell (1963) refer to the posterior projections (see below).

Posterior projections of epiphallus (Dirsh, 1956 [except *Pyrgomorphidae*], 1965) — A pair of lobes extending from the posterolateral margins of the lateral plates of the epiphallus *(Auricula,* Znoĭko, 1928; *Lateral lobes of the epiphallus,* Lal and Parshad, 1961 a, b; *Posterior*

processes (of epiphallus), Barnum, 1959; Rehn and Randell, 1963) — These do not seem to be present as such in *Pyrgomorphidae,* although the 'Externolateral expansions' *(q. v.)* may be homologous. The structures previously termed by Dirsh (1956) "posterior projections of the epiphallus" in *Pyrgomorphidae* are now regarded as being homologous with the lophi *(q. v.).* See also 'Posterior processes of epiphallus'.

Posteroventral expansions of rami of cingulum — Lobe-like rearward deepening of the enlarged apices of the rami, e. g., in some *Geloiini* and *Gymnohippini (Expansions postéro-ventrales des rami,* Descamps and Wintrebert, 1966 b). Term not used in present work.

Pseudoarch (of ectophallus) (Kevan and Akbar, 1963, 1964; Akbar, 1966 b) — A small sclerotized structure lying between the suprarami of the cingulum, posterior to the central membrane of the ectophallus and connecting the bases of the valves of the cingulum with the proximal parts of the aedeagal valves; developed from the ectophallic membrane *(Pseudoarche du cingulum,* Descamps and Wintrebert, 1966 b). This structure seems to be peculiar to *Pyrgomorphidae,* not homologous with the 'arch of the dorsal valves' of Roberts (1941) or 'arch of the cingulum' of Dirsh (1956).

Ramal inflections — See 'Inflections of rami'.

Rami of cingulum (Roberts, 1941; Chopard, 1949; Ander, 1956; Dirsh, 1956, 1961, 1962, 1963 a, 1965 b, c, 1966 a, b; Barnum, 1959; Latif *et al.,* 1959; Hubbell, 1960; Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Lal and Parshad, 1961a, b; Rehn and Eades, 1961a-d; Jago, 1963; Uvarov, 1966) — A pair of large, sclerotized plates forming the lateral and ventral walls of the posterior part of the cingulum, elongated so as to participate in the formations of the ventral cleft; in *Pyrgomorphidae,* usually terminating subventrally in prominent lobes, the 'sheaths' *(q. v.) (Valvae penis* or *Valve del pene,* Berlese, 1882; *Perifallo,* in part, Berlese, 1906; *Valves génitales inférieurs,* Chopard, 1920; *Rami,* Walker, 1922; Descamps, 1966; Descamps and Wintrebert, 1966 b; *Valvae inferiores,* Znoĭko, 1928; Boldyrev, 1929; *Rami of endapophyses,* Hubbell, 1932; *Lateral plates in the proximal part of the dorsal lobes,* Snodgrass, 1935 b; *Subventral valves,* Qadri, 1940; *Lobes latéreaux de la pièce tégulaire,* Grassé and Hollande, 1945; *Lower genital valves* and *Rami of pseudosternite* [*sic*], Ohmachi, 1950; *Rami del cingulum,* Márquez Mayaudón, 1962 [more restricted to parts making up ventral transverse thickening]).

Sheaths of ectophallus — The paired, lobe-like structures extending distally from the rami of the cingulum; partly somewhat sclerotized (here regarded as constituting part of the cingulum) and partly membranous (the portion occupying an area between the rami and suprarami; not regarded here as part of the cingulum proper); the fused ecto- and endophallic membranes are joined to their inner margins so as to form a covering for the distal parts of the 'aedeagus' and are associated with the aedeagal valves *(Prépuce,* in part, Peytoureau, 1895; Chopard, 1920 [not 1949 = pallium]; *Sheath of aedeagus,* in part, Roberts, 1941; Lal and Parshad, 1961 a, b; *Sheath of penis,* in part, Dirsh, 1956, 1961, 1962, 1965 b, 1966 a, b; *Sheath of aedeagal valves,* in part, Rehn and Grant, 1959 b; *Sheath,* Barnum, 1959, in part; Latif *et al.,* 1959; Eades, 1961 a, b, 1962; Gurney and Eades, 1961; Rehn and Eades, 1961 a-d; Kevan and Akbar, 1963, 1964; *Sheath(s) of cingulum,* Kevan, 1966 g; "*S*" [in diagram only], Akbar, 1966 b). For broader use of the term 'Sheath', see 'Aedeagal valves'.

Spermatophore sac (Hubbell, 1932; Else, 1934; Snodgrass, 1935 b; Roberts, 1941; Karandikar, 1942; Uvarov, 1943; Albrecht, 1953, 1956; Ander, 1956; Dirsh, 1956, 1961, 1962, 1963 a, b, 1965 b, c, 1966 [as abbreviation only, 1966 b]; Barnum, Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Lal and Parshad, 1961 a, b; Rehn and Eades, 1916 a-d; Thomas, 1963; Uvarov, 1966) — A large (rarely smaller), expanded endophallic sac, in *Pyrgomorphidae* dorsal to the endophallic sclerites; communicating ventrally with the ejaculatory sac through the (primary or true) gonopore *(Sperm sac,* Else, 1934; *Sacco spermatofore dell'endofallo,* Jannone, 1939; *Sac spermatophorique,* Grassé and Hollande, 1945; *Sac spermatophore,* Chopard, 1949; Descamps, 1966; Descamps and Wintrebert, 1966 b; *Spermatophorensack,* Beier, 1955; *Spermatophoren-Sacculus,* Lux, 1957, 1961; *Saco del spermatóforo,* Márquez Mayaudón, 1962; *Endophallic sac(s),* in part, Jago, 1963; Dirsh, 1966 b; *Sac endophallique,* Descamps, 1966).

Subgenital plate (auctt.) — The externally visible part of the last abdominal sternum, (in male, the 9th); this is usually divided transversely by a goove, when the term is restricted to the distal part of the sternum *(Lamina subgenitalis,* Brunner von Wattenwyl, 1876; *Plaque sous-génitale,* Peytoureau, 1895; Chopard, 1920; Grassé and Hollande, 1945; *Distal plate* [*of 10th sternum*], Snodgrass, 1903; *Hypoproct,* Crampton, 1918; Else, 1934; *Hypandrium,* Crampton, 1918; Walker, 1922; Else, 1934; Snodgrass, 1935 a; *Coxites of ninth ster-*

num, Walker, 1922, *Novasternum,* in part, MacGillivray, 1923; *Subgenitalna plochitsa,* Baranov, 1925; *Subgenitalplatte,* Baranov, 1925; Znoĭko, 1928; Beier, 1955; *Subgenital'naya plastinka,* Znoĭko, 1928; *Lamina sottogenitale,* Guarino, 1935; *Ninth sternal lobe,* Snodgrass, 1935 b; *Syncoxite* (of Crampton), Karandikar, 1942).

Supragenital cavity (Karandikar, 1942) — The space above the epiphallus limited by the epiphallic infold.

Suprarami (of cingulum) (Eades, 1962, 1963) — A pair of (usually) small processes extending dorsally from the rami of the cingulum *(Lóbulo[s] dorsal[es] del aedeagus,* Márquez Mayaudón, 1962).

Suprazygomal plate (of cingulum) (Kevan and Akbar, 1963, 1964; Akbar, 1966 b) — A usually semicircular, sclerotized area lying dorsally at the base of the cingulum, above the zygoma, and providing an attachment for the ectophallic membrane; characteristic of *Pyrgomorphidae;* occasionally lacking *(Dorsal process,* Dirsh, 1956; *Dorsal sclerotization,* Dirsh, 1963 b [*Pyrgohippus*]; *Suprazygoma (of cingulum),* Kevan, 1966 e, g; Akbar, 1966 b; *Plaque sclérifiée* and *Apodème dorsale* [*du cingulum*], Descamps, 1966).

Valves of cingulum (Dirsh, 1956, 1961, 1962, 1963 a, b, 1965 b, 1966 a, b; Barnum, 1959; Hubbell, 1960; Uvarov, 1966) — A pair of very variably shaped and developed structures, often minutely denticulate, arising directly from the cingulum and extending posterodorsally (displaced posteroventrally in some *Verduliini)* from the distal ends of the suprarami or rami and from the central membrane of the ectophallus; connected to each other basally and to the aedeagal valves by the pseudoarch; derived from the ectophallic membrane and thus not part of the endophallus; in *Pyrgomorphidae,* they do not seem to correspond functionally with the valves of the cingulum in other families *([Sclerites of] dorsal lobes,* in part, Walker, 1922; *Frontal valves of penis,* Boldyrev, 1929; *Dorsal lobes of penis,* Hubbell, 1932; Else, 1934; Ohmachi, 1950; *Valve superiori* [*del pene*], Guarino, 1935; *Anterior (dorsal) apical processes of aedeagus,* in part, Snodgrass, 1935 b, 1937; *Lobi esterni del pene,* Jannone, 1936; *Processi dorsali del pene,* Jannone, 1939; *Dorsal valves of aedeagus,* Gurney, 1940; Roberts, 1941; Ander, 1956; Lal and Parshad, 1961 a, b; *Dorsal penis valves,* Qadri, 1940; Albrecht, 1953; [*Dorsal*] *Aedeagal valves,* Roberts, 1941; Uvarov, 1943; *Horn-shaped sclerites,* Karandikar, 1942; *Valves d' oedeagus,* Chopard, 1949; *Anterior process* [*of penis*], Ohmachi, 1850; *Dorsal aedeagal valves,* Albrecht, 1956; Rehn and Grant, 1959 a, b;

Kevan, 1957; *Dorsale Valven,* Lux, 1957, 1961; *Ventral valves (of cingulum),* Latif *et al.,* 1959; *Dorsal penial valves,* Hubbell, 1960; *Ectophallic valves,* Rehn and Grant, 1960 b; *Valves of suprarami,* Eades, 1962; *Cingular valves,* Jago, 1963; *Dorsal valves of penis,* Thomas, 1963; *Cingulum valves,* Kevan, 1965, 1966 f; *Valves du cingulum,* Descamps, 1966; Descamps and Wintrebert, 1966 b).

Valves of ejaculatory sac (Dirsh, 1956) — The regulating mechanism located at the orifice of the ejaculatory duct.

Ventral cleft (of ectophallus) (Kevan and Akbar, 1963, 1964; Akbar, 1966 b) — The ventral, longitudinal opening for the phallotreme and ejaculatory sac of the endophallus, located at the distal end of the cingulum; formed by the union of the continuous ecto- and endophallic membranes with the rami of the cingulum *(Phallotreme cleft,* Snodgrass, 1935 b, in part; Roberts, 1941; Uvarov, 1943; Albrecht, 1953, 1956; Latif *et al.,* 1959; *Slit-like phallotreme,* in part, Snodgrass, 1935 b, 1937; *Cleft,* Roberts, 1941; Dirsh, 1956; *Fente phallotrémique,* in part, Grassé and Hollande, 1945, 1946; *Phallotreme,* in part, Ander, 1956; *Median cleft* or *Cleft of phallotreme,* Hubbell, 1960; *Ventral phallotreme cleft,* Eades, 1961 b, 1962; Rehn and Eades, 1961 a, b, d; *Fente ventrale,* Descamps, 1966). Dirsh (1956) also attributes to Snodgrass (1935 b) the use of the term 'vertical cleft', but that author only used the words in an explanatory way to refer to the phallotreme.

Ventral infold (of ectophallic membrane) (Roberts, 1941; Uvarov, 1943; Dirsh, 1956; Eades, 1961 a, b, 1962; Gurney and Eades, 1961; Rehn and Eades, 1961 a-d) — The membranous invagination extending beneath the anteroventral region of the ectophallus; from its dorsal surface arises the sclerotized ventral process of the cingulum.

Ventral lobe of ectophallic membrane — This and synonymous terms, such as 'ventral lobe of aedeagus', are not applicable to *Pyrgomorphidae* in which the homologous 'lateral lobes of the ectophallic membrane' are not united ventrally.

Ventral lobes of rami of cingulum — A pair of lobes extending posteriorly from the ventral region of the rami in *Pterorthacris.*

Ventral longitudinal thickenings of cingulum (Kevan and Akbar, 1963, 1964; Akbar, 1966 b) — A pair of sclerotized bands extending posteriorly along the ventral part of the cingulum from posteroventral extensions of the basal thickening.

Ventral oblique thickenings of cingulum (Kevan and Akbar, 1963) — A pair of sclerotized bands extending obliquely across the sides of

the cingulum from posterolateral extensions of the basal thickening.

Ventral process (of cingulum) (Dirsh, 1956) — A triangular, subtriangular, or tongue-like, rarely truncated or narrowly elongated, process of variable length, extending forwards from the mid-ventral part of the cingulum; developed from the dorsal surface of the ventral infold of the ectophallic membrane *(Ventral posterior process of cingulum,* Dirsh, 1963 b; *Processus ventral d'ectophalle,* Descamps and Wintrebert, 1966 b).

Ventral processes of apodemal plates (of cingulum) (Kevan and Akbar, 1964) — A pair of small, usually downwardly directed, projections sometimes found at the base of the cingulum, particularly in many *Orthacridini;* possibly representing the true apodemes of the cingulum *(q. v.)* — see also p. 180.

Ventral processes of endophallic apodemes — A pair of lobes or processes sometimes arising ventrally on the endophallic apodemes; usually, but not always, directed forwards.

Ventral transverse thickening of the cingulum (Kevan and Akbar, 1963; Akbar, 1966 b) — A short, transverse, more heavily sclerotized band in the mid-ventral region of the cingulum, joining the two ventral extensions from the basal thickening; often incomplete, sometimes lacking *(Rami del cingulum,* in part, Márquez Mayaudón, 1962).

Zygoma (of cingulum) (Roberts, 1941; Grassé and Hollande, 1945, 1946; Chopard, 1949; Albrecht, 1953, 1956; Ander, 1956; Dirsh, 1956, 1961, 1963 a, c, 1965 b, c, 1966 a, b; Lux, 1957, 1961; Barnum, 1959; Latif *et al.,* 1959; Hubbell, 1960; Eades, 1961 a, b, 1962, 1963; Gurney and Eades, 1961; Lal and Parshad, 1961 a, b; Rehn and Eades, 1961 a-d; Jago, 1963; Descamps, 1966; Descamps and Wintrebert, 1966 b [not used for *Pyrgomorphidae*]) — A usually broad, plate-like structure (in *Pyrgomorphidae),* forming the anterodorsal part of the cingulum; overlaid by the suprazygomal plate, when this is present, and sometimes largely obscured by it *(Face supérieure de la partie intra-abdominale du pénis,* in part, Peytoureau, 1895; *Epifallo,* in part, Berlese, 1906; *Pont postérieur,* Chopard, 1920; *Arch of endapophyses,* Walker, 1922; *Pons posterior,* Znoĭko, 1928; Boldyrev, 1929; Ander, 1956; *Endopophyseal arch,* Hubbell, 1932; *Ponte posteriore,* Guarino, 1935; *Zygoma,* Snodgrass, 1935 b; *Zigomo dell'apodema del pene,* Jannone, 1939; *Transverse sclerotized bar,* Qadri, 1940; *Dorsal valve,* etc., in part, Karandikar, 1942 [see also Cingulum]; *Pont trans-*

versal, Grassé and Hollande, 1945; *Bar of aedeagal apodemes,* Thomas, 1963; *Zygomal plate,* Kevan, 1966 i).

b) *The Female Structures.*

Apical bulb of spermathecal appendage — A small, usually spherical or subspherical swelling at the apex of the spermathecal appendage, when this is present; often lacking *(Troncature brusque* [*de l'éperon*], Fenard, 1896; *Globose swelling* [*of apical diverticulum*], Slifer, 1940 c; *Réservoir secondaire, s. str.,* Voy, 1949; *Pouch* [*of apical diverticulum*], Rehn and Eades, 1961 c; *Small bulb,* Kevan, 1966 f).

Apical diverticulum of spermatheca (auctt.) — An ambiguous term discarded in the present work — see 'Spermathecal appendage'.

Apical pocket of spermatheca — A small lobe-like swelling marking the upper end of the spermathecal vesicle; the caecum of the spermatheca typically arises laterally just below it, but the pocket is often suppressed *(Small secondary evagination of preapical diverticulum,* Slifer, 1940 b; *Preapical diverticulum,* Dirsh, 1957 [but only referring to *Charilaidae* (= *Pamphagodidae), Lathiceridae,* and *Romaleinae*]; *Apical diverticulum* Rehn and Grant, 1959 a, for the most part, 1960 a; *Bulge suggesting presence of second diverticulum,* Dirsh, 1963 b).

Appendage of spermatheca — see 'Spermathecal appendage'.

Body of receptaculum seminis — see 'Spermatheca'.

Caecum of spermatheca — A normally large, sac-like structure of very variable size and form, but, in most *Pyrgomorphidae,* basically S- or C-shaped and arising laterally near the apex of the spermathecal vesicle and initially running in a more or less contrary direction to it; often more or less continuous with the vesicle and thus terminal or subterminal in position; rarely completely lacking *(Réservoir séminal (proprement dit),* in part, Fenard, 1896; *Lower section of receptaculum seminis,* Fedorov, 1927; *Preapical diverticulum,* in part, Slifer, 1939, 1940 a, 1943 a; Katiyar, 1956; Dirsh, 1957 [but only referring to *Acrididae* other than *Romaleinae*], 1963 a, 1965 c; Rehn and Grant, 1959 a, b, 1960 a, c; Gurney and Eades, 1961; Rehn and Eades, 1961 b, c; Gregory, 1965; Uvarov, 1966; [one of two] *Diverticula,* in part, Uvarov, 1943; *Réservoir principal,* in part, Voy, 1949; *Distal diverticulum,* in part, Katiyar, 1956; *Apical diverticulum,* in part, Dirsh, 1957 [only in families except *Charilaidae* (= *Pamphagodidae), Lathiceridae* and *Acrididae* other than *Romaleinae*]; *Diverticulum,* in

part, Rehn and Grant, 1960 b; Dirsh, 1963 b; *Porción distal de la espermateca,* Márquez Mayaudón, 1962 [*Parte apical de la espermateca* = vestigial spermathecal appendage]; *Additional third branch* [*of spermatheca*], Dirsh, 1963 c; *Subterminal diverticulum,* in part, Kevan, 1967 f [in error as 'spermathecal duct' in legend to figures]; *Spermatheca* [*s. str.,* in referring to "small oval vesicle"], Uvarov, 1966).

Columellae (of subgenital armature) (Randell, 1963; Rehn and Randell, 1963; Kevan, 1963, 1966 e; Vickery, 1964, 1967 b; Akbar, 1966 a, in part) — small, paired, sclerotic structures on the floor of the genital chamber, situated near the base of the egg-guide; vertically connecting the postvaginal sclerite with the upper surface of the subgenital plate *(Ridgelike outgrowths* or *elevations,* Karandikar, 1942; *Jannoné's organs,* Agarwala, 1952 a, in part, 1952 b, 1953, 1954, in part; Thomas, 1965, Uvarov, 1966; *Sclerotic tubercles,* Agarwala, 1952 a; *Chitinbrücken,* Lux, 1957, 1961; *Columelle*[*s*] and *Petites sclérites épais,* Descamps, 1966).

Constricted tube (of spermathecal duct) (Gregory, 1965; Uvarov, 1966) — The narrow, inner spiral of the spermathecal duct immediately below the spermatheca, around which it is usually coiled; its lower limit is marked by the 'Reverse bend of the thin tube' *(q. v.)* (*Tortillon,* approximately, Fenard, 1896; Voy, 1949; *Short, anterior, straight part,* Snodgrass, 1903; *Gewinde des Receptaculum seminis,* in part, Sokolow, 1926; *Tubo collegato,* approximately, Paoli, 1937; *Innere Spirale,* Mika, 1959).

Contact areas (of subgenital armature) (Randell, 1963; Rehn and Randell, 1963; Vickery, 1964, 1967 a, b) — Restricted, usually somewhat heavily pigmented areas of the post-vaginal sclerite surrounding the columellae and associated with the insertion of the lophi of the male epiphallus *(Parties centrales plus chitinisées de ces lobes* [i. e. de la lame bilobée du huitième sternite], Peytoureau, 1895; *Pigmentflecken,* in part, Sokolow, 1926; *Brown patches* or *Jannone's organs,* in part, Agarwala, 1952 a, 1954 [as "Br. P."]; *Darker regions,* Thomas, 1965). The term is used here for specialized areas of the post-vaginal sclerite of certain *Pyrgomorphidae* that lack columellae; these areas may not be strictly homologous with those of the *Acrididae.*

Egg-guide (Packard, 1878; Comstock and Kellogg, 1899; Snodgrass, 1903; MacGillivray, 1923; Snodgrass, 1935 a, b; Qadri, 1940; Karandikar, 1942; Gupta, 1950, Agarwala, 1952 a, b, 1953, 1954;

Albrecht, 1953; Ander, 1956; Thomas, 1963, 1965; Randell, 1963, Rehn and Randell, 1963; Kevan, 1963, 1966 b, e, g, h; Vickery, 1964, 1967 b; Uvarov, 1966) — The median, usually triangular, process at the posterior margin of the subgenital plate *(Appendice dell'ottavo arco,* Berlese, 1882; *Languette médiane,* Chopard, 1920; *Subgenitale Platte* or *Subgenitalplatte,* Sokolow, 1926; *Digitulus,* Boldyrev, 1929; *Lobo mediano,* Guarino, 1935; *Mucrone terminale mediano* or *Guida dell' uovo,* Paoli, 1937; *Estroflessione subconiforme posteriore della lamina sottogenitale,* Jannone, 1939; *Mittlerer Fortsatz,* Lux, 1957, 1961; *Guideoeuf,* Descamps, 1966).

Final bend of spermathecal duct — That part of the spermathecal duct at which the 'Thin tube' bends and widens into the 'Thick tube' *(Spirale,* in part, Fenard, 1896; *Spire terminale,* in part, Voy, 1949; *Grosse Schlinge,* in part, Mika, 1959; *First bend,* Gregory, 1965).

Floor pouches (of genital chamber) (Agarwala, 1952 a, b, 1953, 1954; Vickery, 1967 b) — A pair of crescentic, membranous invaginations lying above and partially covering the base of the post-vaginal sclerite *(Membrane de ces lobes* [i. e. de la lame bilobée du huitième sternite], Peytoureau, 1895; *Secondary pockets,* Nel, 1929; *Lateral pouches,* Nel, 1929; Thomas, 1965; *(Pocket-like) depressions* plus *Intermediate membrane,* Karandikar, 1947; *Drüsentaschen,* Lux, 1957, 1961; *Pockets,* Thomas, 1963; *Tunic,* Randell, 1963; Rehn and Randell, 1963; Kevan, 1963, 1966 b; Vickery, 1964; Akbar, 1966 a; *Tunica,* Kevan, 1966 g).

Genital chamber (auctt.) — The space lying above the subgenital plate and below the ovipositor valves, into which the common oviduct discharges *(Bursa copulatrix,* Snodgrass, 1903; *Cavité sous-génitale,* Chopard, 1920; *Genatasinus* or *Genital pouch,* MacGillivray, 1923; *Genital cavity,* Nel, 1929; *Genitaltasche,* Weber, 1933; *Under-folded distal region of 8th sternite,* Karandikar, 1942; *Gynatrium,* Gupta, 1950; *Genitalkammer,* Beier, 1955; Lux, 1957, 1961; *Chambre génitale,* Descamps, 1966).

Head of receptaculum seminis — See 'Spermatheca'.

Inner spiral of spermathecal duct — See 'Constricted tube'.

Jannone's organs (Agarwala, 1952 a, 1954, both in part; Vickery, 1964) — The 'Collumellae' together with the 'Contact areas' of the subgenital armature *(q. v.) (Jannon'schen Organen,* Lux, 1957, 1961). In its original usage this terms is ambiguous (see p. 195); it is best avoided.

Lateral appendage of spermathecal duct — See 'Spermathecal appendage'.

Median longitudinal groove (of ovitract) — A furrow separating the floor-pouches and lying a short distance in front of the base of the egg-guide *(In die Scheide führende Rinne,* approximately, Sokolow, 1926; *Longitudinal groove* or "groove extending along the mid-longitudinal line of the egg-guide and anterioly between the floor pouches", Agarwala, 1952 b).

Orifice of spermathecal duct — The opening of the duct of the receptaculum seminis which first receives the spermatophore from the male; anatomically the termination of the spermathecal duct, not the beginning as it is often regarded *(Opening of bursa copulatrix,* Comstock and Kellogg, 1899; *Opening of spermatheca,* Snodgrass, 1903; Vardé, 1934; Agarwala, 1952 a; *Aperture of spermatheca,* Walker, 1919; *Spermora,* MacGillivray, 1923; *Äussere Öffnung des Receptaculum seminis,* Sokolow, 1926; *Ostium receptaculi seminis,* Fedorov, 1927; *Orificium spermathecae,* Boldyrev, 1929; *Spermathecal pore,* Nel, 1929; *Orifice de la spermathèque,* Vardé, 1929; *Orifice of spermatheca,* Snodgrass, 1935 a; *Opening of spermathecal duct,* Snodgrass, 1935 b; Slifer, 1939; Thomas, 1963; *Spermathecal aperture,* Snodgrass, 1935 b; Albrecht, 1953, 1956; Gregory, 1965; Uvarov, 1966; *Apertura della spermatheca,* Janonne, 1939; *Spermathecal opening,* Slifer, 1939; Karandikar, 1942; Thomas, 1965; *Pore of spermathecal duct,* Katiyar, 1956; *Eingang Receptaculi seminis,* Mika, 1959; *Orificio espermatecal,* Márquez Mayaudón, 1962).

Ovitract (Akbar, 1966 a) — The V-shaped area behind the vaginal opening and in front of the egg-guide, formed by the median parts of the floor pouches and incorporating the median longitudinal groove (q. v.).

Posterior edge (of subgenital plate) (Agarwala, 1952 a, b, 1953, 1954; Randell, 1963; Vickery, 1967 b) — The posterior margin of the 8th abdominal sternum where it is folded anteriorly to form the floor of the genital chamber *(Fused edge,* Agarwala, 1952 b, 1953, 1954; *Posterior border,* Agarwala, 1952 b; Akbar, 1966 a; *Fusion edge,* Vikkery, 1964; *Thickened region,* Thomas, 1965; *Bord postérieur,* Descamps, 1966; *Posterior margins,* Akbar, 1966 a).

Post-vaginal sclerite (of subgenital armature) (Randell, 1963; Kevan, 1963, 1966 b, g) — A thin, sclerotized, but largely unpigmented, plate-like structure lying on the floor of the genital chamber, posterior

to the opening of the common oviduct or vagina, and the floor pouches; usually fused with the subgenital plate; in *Pyrgomorphidae* and other families with a bridge-like male epiphallus it is divided into two lateral areas narrowly connected at the base of the egg-guide *(Lame bilobée due au repli postérieur du huitième sternite,* Peytoureau, 1895; *Aires triangulaires* [*de la membrane tapissant la face de la plaque sous-génitale*], Chopard, 1920; *Inner reflexed surface of subgenital plate,* in part, Nel, 1929; *Chitinous concave* or *Underfolded plates,* Karandikar, 1942; *Post-vaginal sclerotic areas* [when weakly sclerotized], Randell, 1963; *Post-vaginal sclerites* [plural], Rehn and Randell, 1963; Akbar, 1966 a; *Floor of genital chamber,* Vickery, 1964 [other authors have used this only as a general expression]; *Membrane de la chambre génitale,* Descamps, 1966).

Principal seminal reservoir — The spermathecal vesicle together with the caecum of the spermatheca *(Réservoir séminal (proprement dit),* Fenard, 1896; *Lower section of receptaculum seminis,* Fedorov, 1927; *Spermatheca* [*s. str.*], Nel, 1929; *Preapical diverticulum,* Slifer, 1939, 1940 a, 1943 a, Katiyar, 1956; Dirsh, 1957 [only in *Acrididae* other than *Romaleinae*]; Rehn and Grant, 1959 a, b, 1960 a, c; Gurney and Eades, 1961; Rehn and Eades, 1961 b, c; Eades, 1962; Gregory, 1965; [one of two] *Diverticula,* Uvarov, 1943; *Réservoir principal,* Voy, 1949; *Distal diverticulum,* Katiyar, 1956; *Apical diverticulum,* Dirsh, 1957 [only in *Romaleinae* and in families other than *Acrididae*]).

Receptaculum seminis (Berlese, 1908; Sokolow, 1926; Fedorov, 1927; Weber, 1933; Snodgrass, 1935 a; Lux, 1957, 1961; Mika, 1959) — The entire spermatheca, in the sense here used, together with its duct *(Vesiciola seminale,* Berlese, 1882; *Poche copulatrice,* Peytoureau, 1895; *Spermatheca* [*sens. lat.*], Snodgrass, 1903; Walker, 1919; Boldyrev, 1929; Weber, 1933; Vardé, 1934; Snodgrass, 1935 a; Slifer, 1939, 1940 a-c, 1943 a; Qadri, 1940; Uvarov, 1943, 1948, 1966, in part; Gupta, 1950; Katiyar, 1956; Dirsh, 1957, 1961, 1963 a-c; 1964 a; 1965 c; Rehn and Grant, 1959 a-c, 1960 a-c; Eades, 1961 a, 1962; Gregory, 1965; Kevan, 1966 h; *Ricettaculo seminale, Spermoteca* or *Spermateca,* Berlese, 1908; *Spermathèque,* Vardé, 1929; Descamps, 1966; Descamps and Wintrebert, 1966 b; *Réceptacle séminal,* Chopard, 1949). For other uses of term 'Receptaculum seminis' see 'Spermatheca'.

Reverse bend of thin tube of spermathecal duct — The part of the

duct at which the 'Constricted tube' reverses its direction of coil and becomes the 'Thin tube'.

Secondary diverticula of spermathecal appendage — Pocket-like, or branch-like elaborations, normally of the outer side of the spermathecal appendage (i. e. of the side away from the spermathecal vesicle); usually located on the lower part of the appendage but sometimes on the vestibule or even lower on the spermathecal duct *(Slender knob, Lateral swelling* and *Lateral projection* [*of apical diverticulum*], Slifer, 1940 c; *Secondary diverticula of spermatheca, Vermicular diverticula, Lateral bulges* or *Pocket-like bulges* or *diverticula,* all in part, Dirsh, 1957; *Supplementary diverticula,* Rehn and Grant, 1959 b).

Secondary diverticula of (caecum of) spermatheca (Slifer, 1940 a; Dirsh, 1957, in part) — Pocket-like, lobe-like, or branch-like elaborations of the spermathecal caecum, usually on its abapical side; sometimes continuing on the adjacent part of the spermathecal vesicle *(Vermicular diverticula,* etc., in part, as indicated above, Dirsh, 1957; *Pockets (of diverticulum),* Dirsh, 1963 b).

Secondary receptaculum seminis — See 'Spermathecal appendage'.

Secondary spermatheca — See 'Apical bulb of spermathecal appendage'.

Secondary spermathecal duct — The spermathecal appendage without the apical bulb, when the two are differentiated.

Spermatheca [*sensu stricto*] (Comstock and Kellogg, 1899; MacGillivray, 1923; Nel, 1929, in part; Albrecht, 1953, 1956; Beier, 1955; Ander, 1956; Gurney and Eades, 1961; Rehn and Eades, 1961 b, c; Rehn and Randell, 1963; Thomas, 1963, 1965; Kevan, 1966 g, h, 1967) — Those parts of the receptaculum seminis other than the spermathecal duct, i. e., the 'body' or 'head of the receptaculum' *(Sebific, Colleterial* or *Sebaceous gland,* Packard, 1878; *Spermoteca,* Berlese, 1882, 1908, in part; *Glandular sac* [*of spermatheca*], Snodgrass, 1903; *Spermateca,* Berlese, 1908; Jannone, 1939; *Receptaculum seminis,* Berlese, 1908; Beier, 1955; *Recittaculo seminale,* Berlese, 1908; *Réservoir séminal* [*sens. lat.*], Fénard, 1896; Chopard, 1949; *Endkämmerchen,* Sokolow, 1926; Mika 1959; *End ball of receptaculum,* Fedorov, 1927; *Upper chamber of spermatheca,* Boldyrev, 1929; *Samenkapsel,* Weber, 1933; Lux, 1957, 1961; *Terminal section of spermatheca,* Snodgrass, 1935 b; *Terminal sac* [*of spermatheca*], Qadri, 1940; *Distal end of spermatheca,* Slifer, 1940 c; Rehn and Grant, 1959 b, c; *Tip of spermatheca,* Slifer, 1940 c; *Endkörper,* Lux, 1957,

1961; *Distal diverticula,* Rehn and Grant, 1959 b; *Endbläschen* or *Eigentliches Receptaculum seminis,* Mika, 1959; *Diverticulum,* Rehn and Grant, 1960 b; *Espermateca,* Márquez Mayaudón, 1962; *Apical portion of spermatheca,* Uvarov, 1966). For other uses of term 'spermatheca' see 'Receptaculum seminis'.

Spermathecal aperture — See 'Orifice of spermathecal duct'.

Spermathecal appendage (Kevan, 1966 g) — Basically duct-like structure opening into the primary spermathecal duct, usually just below the spermathecal vesicle and frequently into the vestibule; it may represent the left member of primitively paired receptacula seminis; it comprises typically an elongate section, or secondary spermathecal duct, and a small apical bulb, or secondary spermatheca; when present in *Pyrgomorphidae* it has most usually shifted upward so as to take up a position on the principal reservoir, frequently having migrated to become a subterminal appendage of the caecum; rarely (some *Nereniini).* it retains a more primitive position well down on the primary spermathecal duct (when it may be termed *Lateral spermathecal appendage);* it may be lobed or even branched *(Éperon,* Fénard, 1896; Voy, 1949; *Ghiandole spermofile,* Berlese, 1908 [not specifically in *Orthoptera*]; *Upper section of receptaculum seminis,* Fedorov, 1927; *Spermathecal gland,* Nel, 1929; Snodgrass, 1935 a [in generalized insect]; *Receptaculardrüse,* Weber, 1933; *Apical diverticulum of spermatheca,* Slifer, 1939, 1940 a-c, 1943 a; Katiyar, 1956; Dirsh, 1957 [only *Acrididae, s. str.,* other than *Romaleinae*], 1963 a, 1965 c; Rehn and Grant, 1959 a [a few genera only where well developed], 1959 b, 1960 a; Gurney and Eades, 1961; Rehn and Eades, 1961 b, c; Uvarov and Dirsh, 1961; Eades, 1962; Gregory, 1965; [one of two] *Diverticula,* Uvarov, 1943; *Réservoir secondaire* [*sens. lat.*], Voy, 1949; *Anhangsdrüse* [*des Receptaculum seminis*], Beier, 1955; *Glandular appendix of diverticulum,* Ander, 1956; *Preapical diverticulum,* Dirsh, 1957 [*Pauliniidae* only], 1963 b [*Ambrositracris* only — abnormality or artifact]; *Secondary diverticula,* in part, Dirsh, 1957; *Diverticulum* [one of two], Dirsh, 1963 b [*Atractomorpha* only]; *Parte apical de la espermateca,* Márquez Mayaudón, 1962 [vestige at apex of caecum]; [*Part of*] *two-branched diverticulum,* Dirsh, 1963 c; *Vermicular diverticulum of spermathecal duct,* Dirsh, 1964 a [lateral appendage in *Modernacris* only]; *Subterminal diverticulum,* in part, Kevan, 1966 f [in error, 'spermathecal duct' in captions to figures]; *Lateral diverticulum of spermathecal duct,* Kevan, 1966 g).

Spermathecal caecum — See 'Caecum of spermatheca'.

Spermathecal duct (auctt.) — That part of the receptaculum seminis other than he spermatheca and any lateral spermathecal appendage *(Sebific duct,* Packard, 1878; *Condotto [della spermotteca],* Berlese, 1882; *Canal [de la poche copulatrice],* Peytoureau, 1895; *Canal séminal,* Fenard, 1896; Voy, 1949; *Peduncolo* or *Tubolo [della spermoteca],* Berlese, 1908; *Rohr des Receptaculum seminis,* Sokolow, 1926; *Canal of spermatheca,* Boldyrev, 1929; *Canal de la spermathèque,* Vardé, 1929; *Ductus receptaculi,* Weber, 1933; *Condotto della spermateca,* Jannone, 1939; *Convoluted tube [of spermatheca],* Qadri, 1940; *Canal [séminal],* Chopard, 1949; *Gewundener Schlauch,* Lux, 1957, 1961; *Conducto [espermatecal],* Márquez Mayaudón, 1962).

Spermathecal valve — See 'Valve of spermathecal duct'.

Spermathecal vesicle — That part of the spermatheca of a non-appendicular, non-caecal, non-ductal nature immediately above the vestibule; frequently not clearly differentiated from the caecum of the spermatheca, which, in the absence of an apical pocket, may be a continuation of it *(Preapical diverticulum,* in small part, Slifer, 1939, 1940 a-c, 1943 a, and subsequent authors [see under Principal seminal reservoir]; *Réservoir principal,* in small part, Voy, 1949; *Porción basal de la espermateca,* Márquez Mayaudón, 1962 [part of] *Two-branched diverticulum,* Dirsh, 1963 c; *Ellipsoidal shaped chamber (of spermatheca),* Dirsh, 1964 a, [*Modernacris* only]; Kevan, 1966 f, g).

Subgenital armature (Kevan, 1966 a-c, g, h) — The ventral sclerotic and membranous structures lying within the genital chamber, together with the egg-guide *(Armature genitale,* in part, Peytoureau, 1895; *Female copulatory armature,* Randell, 1963; Rehn and Randell, 1963; Akbar, 1966 a; *Armature of subgenital plate,* Vickery, 1964).

Subgenital plate (auctt.) — The eighth abdominal sternum (in the female) including the egg-guide *(Lamina subgenitalis,* Brunner von Wattenwyl, 1876; Beier, 1955; *Huitième urite* or *sternite,* Peytoureau, 1895; *Plaque sous-génitale,* Peytoureau, 1895; Chopard, 1920; Vardé, 1929; Descamps, 1966, Descamps and Wintrebert, 1966 b; *Octasternum,* MacGillivray, 1923; *Lamina sotto genitale,* Guarino, 1935; *Subgenitalplatte,* Lux, 1957, 1961). Note, Sokolow's (1926) equivalent terms refer only to the egg-guide.

Terminal dilation of spermathecal duct — The swollen end of the terminal part of the spermathecal duct immediately above the orifice; not always differentiated *(Bursa copulatrix,* Packard, 1878; Comstock

and Kellogg, 1899; Vardé, 1929; *Camera prevulvare* or *Cella praevulvaria,* Berlese, 1882, 1908; *Zone indurée,* Peytoureau, 1895; *Dilated part of receptaculum,* Fedorov, 1927; *Expansión del conducto espermatecal,* Márquez Mayaudón, 1962; *Base of spermathecal duct,* in part, Uvarov, 1966).

Terminal part of spermathecal duct — The 'Thick tube', together with the 'Terminal dilation', if present *(Proximal end* or *portion of spermathecal duct,* Slifer, 1939, 1940 a, b, 1943 a).

Thick tube (of spermathecal duct) (Gregory, 1965; Uvarov, 1966) — The thick-walled, typically uncoiled part of the spermathecal duct above the 'Terminal dilation' (if present) or immediately above the orifice (if dilation absent); merges into the 'Thin tube' at the 'Final bend' *(Renflement sus-oviductal,* Fenard, 1896; *Posterior straight part,* Snodgrass, 1903; *Tubo crasso,* Paoli, 1937; *Proximal end* or *portion of spermathecal duct,* in part, *Slifer,* 1939, 1940 a, b, 1943 a; *Ductus receptaculi,* Mika, 1959).

Thin tube (of spermathecal duct) (Gregory, 1965; Uvarov, 1966) — The narrow, typically coiled part, or outer spiral, of the spermathecal duct between the 'Final' and 'Reverse bends' *(Spirale* plus *Canal séminal filiforme,* Fenard, 1896; *Median coiled part,* Snodgrass, 1903; *Gewinde des Receptaculum seminis,* in part, Sokolow, 1926; *Middle part of spermatheca,* approximately, Snodgrass, 1935 b; *Tubo tenue,* Paoli, 1937; *Spire terminale* plus *Canal,* Voy, 1949; *Schleife,* Lux, 1957, 1961; *Äussere Spirale,* Mika, 1959).

Valve of spermathecal duct (Kevan, 1966 g) — A small, thickened, often locally sclerotized area (or areas) within the orifice of the spermathecal duct (covers *Lippen des Receptaculum seminis,* Sokolow, 1926; *Small chitinous plate,* Nel, 1929; *Heart-shaped sclerite* and *Triangular sclerites,* Snodgrass, 1935 b; *Spermathecal sclerite,* Slifer, 1939; *Triangular sclerotized plate,* Gregory, 1965; *Horseshoe-shaped sclerite,* Thomas, 1965; *Base of spermathecal duct,* in part, Uvarov, 1966).

Vestibule (of spermatheca) (Gregory, 1965; Uvarov, 1966) — A somewhat widened part of the spermathecal duct lying between the constricted tube and the spermathecal vesicle, usually uninterruptedly confluent with these; sometimes marked off by the junction of the spermathecal appendage with the main spermathecal duct.

c) *List of Abbreviations.*

The following is a list, arranged alphabetically, of the abbreviations used in the illustrations and text of the present part of this study. The majority of the abbreviations used for the male structures are the same as have been used previously in publications referred to on pp. 172-173 — see particularly, Kevan and Akbar (1963: 410, fig. 1; 415, fig. 2; 420, fig. 3; 1964: 1531, fig. 5) Other abbreviations previously used by the two senior authors will be used in future parts of this study but are not included here. Some of the abbreviations for female structures have also been used previously by Kevan (1963; 1966 b, f, g).

A, Appendix of epiphallus (= OS in groups other than *Pyrgomorphidae).*
AB, Apical bulb of spermathecal appendage.
AC, Apodemal plate of cingulum *(Pyrgomorphidae,* Fig. 1 *D);* Apodeme of cingulum (non-*Pyrgomorphidae,* Fig. 1 *C).*
AE, Aedeagus.
AN, Ancora of epiphallus.
AP, Anterior projection of epiphallus.
APO, Apical pocket of spermatheca.
AS, Aedeagal sclerite.
AV, Aedeagal valve.
B, Bridge of epiphallus.
BF, Basal fold of ectophallic membrane.
C, Columella of female subgenital armature.
CA, Contact area of female subgenital armature; also Arch of cingulum in male non-*Pyrgomorphidae.*
CM, Central membrane of ectophallus.
CT, Constricted tube or inner spiral of spermathecal duct (Fig. 2 only).
CV, Valve of cingulum.
E, Epiphallus.
EA, Endophallic apodeme.
ED, Ejaculatory duct.
EG, Egg-guide.
EI, Epiphallic infold.
EM, Ectophallic membrane.

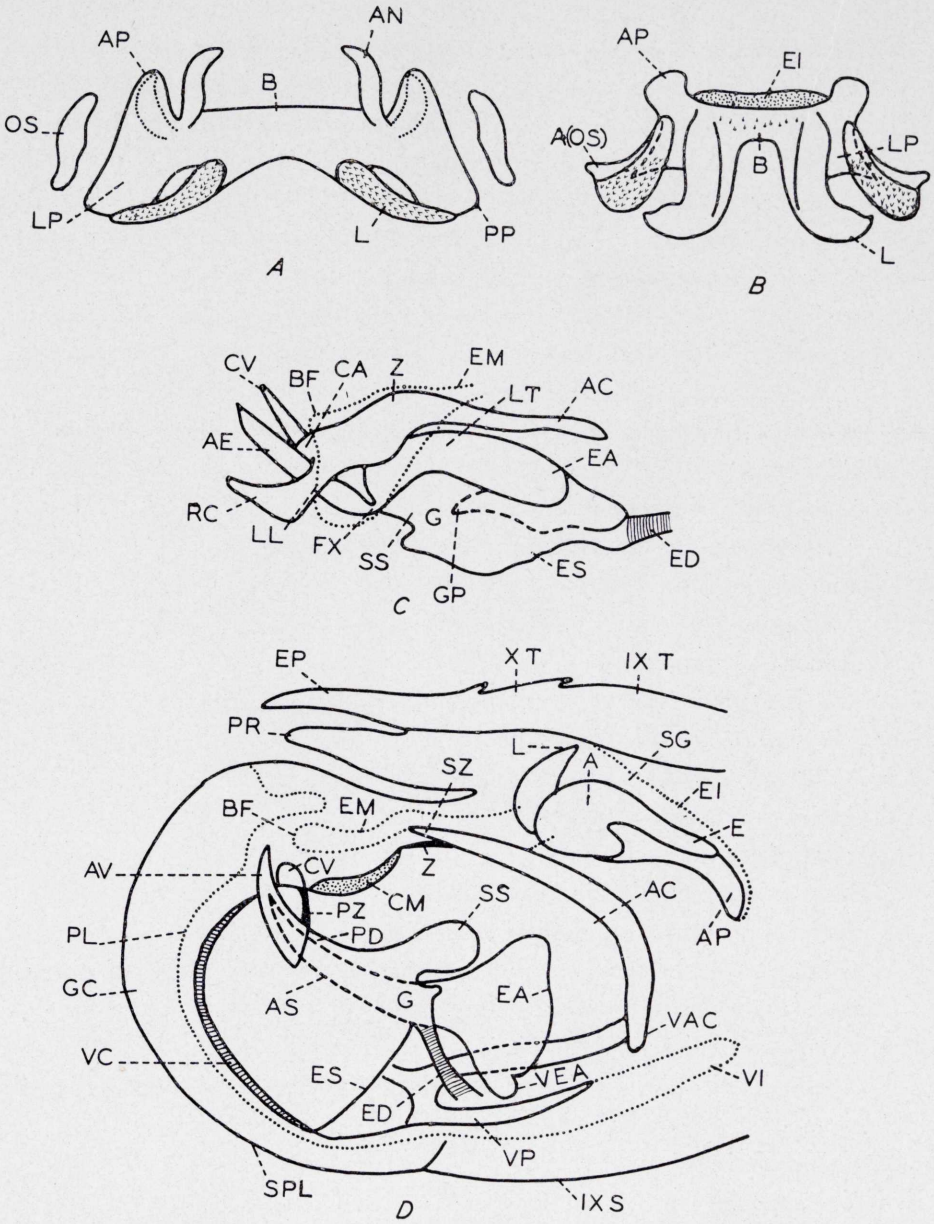

Fig. 1.—Schematic acridoid phallic structures: *A*, generalized acridid epiphallus, dorsal; *B*, generalized pyrgomorphid epiphallus, dorsal; *C*, generalized acridid phallic complex, from right; *D*, generalized pyrgomorphid phallic complex *in situ*, from right. For explanation of notation, see pp. 174-185.

EP, Epiproct.
ES, Ejaculatory sac.
FB, Final bend of spermathecal duct.
FP, Floor pouch of female genital chamber.
FX, Flexure of aedeagal sclerite.
G, Gonopore (male).
IXS, Ninth abdominal sternum of male.
IXT, Ninth abdominal tergum of male.
L, Lophus of epiphallus.
LL, Lateral lobe of ectophallic membrane.
LP, Lateral plate of epiphallus.
T, Lateral plate of endophallic sclerite.
MLG, Median longitudinal groove of ovitract.
O, Orifice of spermathecal duct.
OS, "Oval sclerite" = A.
PD, Phallotreme duct.
PE, Posterior edge of female subgenital plate.
PL, Pallium.
PP, Posterior projection of epiphallus (non-*Pyrgomorphidae*).
PR, Principal seminal reservoir of epiphallus.
PVS, Post-vaginal sclerite of female genital chamber.
PZ, Pseudoarch of ectophallus.
RB, Reverse bend of thin tube of spermathecal duct.
RC, Ramus of cingulum.
SA, Spermathecal appendage; the 'apical diverticulum' and homologous diverticula of previous authors.
SB, Secondary diverticulum of caecum of spermatheca or occasionally or spermathecal vesicle.
SC, Caecum of spermatheca; with (part of) the spermathecal vesicle is the 'preapical diverticulum' of previous authors.
SD, Spermathecal duct [SD of Kevan (1966 f) = "spermathecal diverticulum" — not "spermathecal duct" as erroneously given in the caption].
SG, Supragenital cavity.
SL, Secondary diverticulum of spermathecal appendage (or occasionally of spermathecal duct).
SP, Spermathecal vesicle.
SPL, Subgenital plate.
SS, Spermatophore sac.

SV, Valve of spermathecal duct.
SZ, Suprazygomal plate of cingulum.
TD, Terminal dilation of spermathecal duct.
TP, Thick tube (or terminal part) of spermathecal duct.
TT, Thin tube of spermathecal duct.

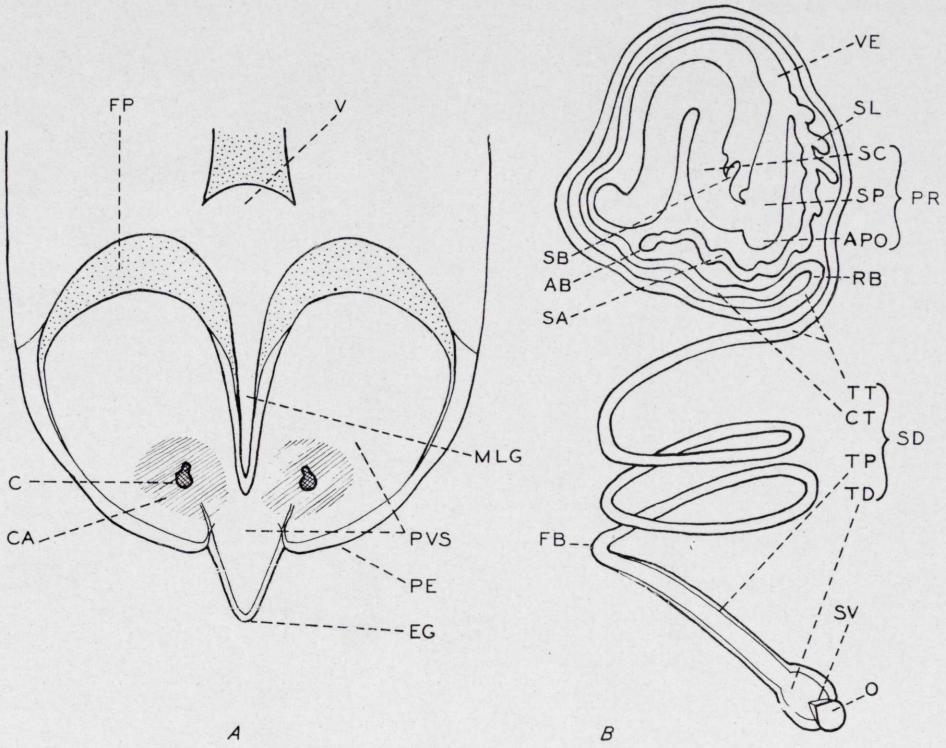

Fig. 2.—Schematic acridoid female structures: *A*, generalized subgenital plate, dorsal; *B*, generalized receptaculum seminis. For explanation of notation, see pp. 193-195, 207-211.

V, Vulva, or Opening of vagina or Common oviduct, or Female gonopore.
VAC, Ventral process of apodemal plate of cingulum (? = vestige of true apodeme of cingulum, see AC).
VC, Ventral cleft of cingulum.
VE, Vestibule of spermatheca.
VEA, Ventral process of endophallic apodeme.
VI, Ventral infold of ectophallic membrane.

VP, Ventral process of cingulum.
XT, Tenth abdominal tergum.
Z, Zygoma of cingulum.

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